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Studies on the Mass Culture of *Phaeodactylum*

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ABSTRACT

Mass cultures of *Phaeodactylum* varying from 15 to 2,400 L have been successfully grown in covered tanks outside the laboratory. The maximum concentration obtained was 32,000 cells/mm^3. Light has been shown to be a severely limiting factor in dense cultures. On the exponential phase of growth, under maximal light conditions, the highest division rate was 1 division in just under 24 hours. Addition of CO_2 has a markedly beneficial effect on maximum cell densities. Phosphate was taken up with extreme rapidity in dense mass cultures; repeated addition of N and P prolonged growth, provided CO_2 was added. A flagellate (*Monas* sp.) occurred regularly and became a predator in aging *Phaeodactylum* cultures. The monad multiplied only slowly in rapidly growing *Phaeodactylum* cultures. Some estimates are given of the dry weight of crop.

INTRODUCTION

In natural bodies of water one of the factors limiting continuous primary production of organic matter is usually a deficiency of mineral salts. For some years it has been the practice to increase the productivity of freshwater fishponds by the addition of fertilizers, mainly inorganic nitrogen and phosphorus compounds. Fertilizers have also been employed in the culture of the freshwater alga *Chlorella* in small-scale industrial plant, where the alga has been grown in densities sufficient for harvesting (cf. Burlew 1953).

Early attempts to raise the productivity of seawater by fertilization of relatively enclosed natural areas were directed towards increasing the production of oysters and fish (Gross, Marshall, Orr, and Raymont 1947; Gross, Nutman, Gauld, and Raymont 1950). The results showed a rapid disappearance of the nitrate and phosphate added which was correlated with an increase in the standing crop of plankton, an increase in bottom fauna density, and an increased rate of growth of fish.

Later work on fertilization of seawater was concerned mainly with the increase in density of the phytoplankton crop. Thus work at Woods Hole by Edmondson and Edmondson (1947) involving the use of both concrete tanks and a natural salt water pond showed that the utilization of phosphate and nitrate resulted in an appreciable increase in the standing phytoplankton crop. In further tank experiments reported by Pratt (1949) increases in phytoplankton also occurred, but the phosphate concentrations could remain high for an appreciable time; sometimes there was an initial lag of up to 3 or 4 weeks before there was a noticeable positive effect on the phytoplankton. Edmondson (1955) found a very rapid rise in photosynthetic rate with fertilization, but cell population increase could lag behind.

Experiments such as these in artificial ponds avoid some of the difficulties that attend investigations on natural bodies of water. Such difficulties include the complexity of the food chains in the sea, and the loss of fertilizers to the bottom deposits and to the outside seawater. But even with tank experiments sampling plankton as an

index of production estimates, in fact, only the standing crop. A stricter estimate of production might be obtained if only a single member of the phytoplankton was cultivated and all zooplankton grazers were excluded.

It was decided to study the effect of fertilization on the production of a single species of phytoplankton is an isolated tank of seawater freed of any zooplankton population. The species selected was *Phaeodactylum tricornutum* (Bohlin). This alga was the only one tested that was found to grow well under tank conditions. Also *Phaeodactylum* has been widely used as a food for zooplankton and, therefore, appeared to be a suitable food species for later large-scale culture. Above all, many experiments on conditions affecting the growth rate of this alga, reported previously as *Nitzschia closterium* var. *minutissima*, have been made in small-scale laboratory cultures over short periods of time, and the alga has been found to be tolerant of large changes of pH and capable of growth over a wide temperature range (Barker 1935, Spencer 1954). It appeared, therefore, to be a relatively unexacting species, well suited for preliminary attempts at mass culture.

No large-scale work could have been attempted without the constant interest and help of the Superintendent and staff of the Central Electricity Authority, Poole. We are indebted to them for the construction of concrete tanks, and for numerous facilities, during the work. Our thanks are also due to several members of the Poole and District Technical Group, especially to Dr. G. D. Muir and Messrs. Hill, Pitman, Wood, Lander, and Benstead, and also to Mr. A. R. Hockley of the Zoology Department, University of Southampton, for their advice and unfailing assistance with sampling and analyses. British Drug Houses Limited and Hamworthy Engineering Limited kindly loaned equipment. Finally we are indebted to D.S.I.R. for a grant in respect of a research assistant.

MATERIALS AND METHODS

Cultures were first grown in concrete tanks built in the grounds of the Central Electricity Authority Generating Station at Poole, Dorset, England. This site was selected because it was hoped later to use scrubbed flue gas from the Station boiler outlet as a source of CO_2 to stimulate phytoplankton growth.

Each concrete tank (5 × 5 × 4 ft. deep) sloped down at the bottom to a central drainage channel leading to an outlet pipe. This was closed inside and outside with rubber bungs. The tanks were painted on the inside with black "Bituros" paint and were covered with a sloping roof of "Windolite" supported on wooden frames and fastened down with bolts. The tanks were filled to a depth within 6 in. of the top when the total volume of medium per tank was about 2,400 L.

In the early experiments no extra lighting was provided, but later on artificial lighting was supplied over the night hours by suspending a cluster of four 100-Watt bulbs under reflectors in the center of a tank.

Throughout the experiments there was no attempt to regulate temperature, which varied from 3° to 25°C over the year (1954/55).

Light measurements were made inside the tank covers in various positions and compared with measurements of the incident light outside the tanks at the same time by means of a pair of matched photoelectric cells. The cell used inside the covers was housed in a watertight metal casing, and could be suspended at known depths under the water surface. The approximate level of the compensation depth (the depth at which the amount of organic matter fixed by the phytoplankton in photosynthesis balances that broken down in respiration) was determined in the tanks. Bottles of culture in the exponential phase of growth were suspended diagonally across the tank at known depths and left for 24 hours. The oxygen concentration was determined by the Winkler technique. No dark bottles were used, so that the differences between the initial and final O_2 concentrations were not corrected for bacterial respiration. They did, however, give an estimate of the production of organic matter which could be correlated with the amount of light

energy received by the culture, since light measurements were made throughout the day at depths at which the bottles were suspended.

Later cultures were grown in glass battery jars containing 15 L of culture medium. These were normally placed in one of the concrete tanks, either on a shelf of wooden slats about 18 in. from the bottom or directly on the bottom of a tank. Artificial lighting could be provided. Temperature variation was from 3° to 30°C in these battery jar experiments.

Some attempts were made in battery jar cultures to regulate the hydrogen-ion concentration by bubbling "pure" CO_2 from a cylinder through the media. It was found more convenient then to transfer the battery jars to the roof of the Generating Station. They were placed in a position such that they were never exposed to direct sunlight; no artificial lighting was provided in these experiments.

The culture medium was prepared from coarsely filtered seawater taken from Holes Bay, Poole, near the Generating Station inlet pipes. The salinity at the inlet varied usually between 28‰ and 34‰. Many methods of sterilization were considered initially, such as hydrogen peroxide treatment and ultra-violet light. Finally chlorine sterilization was carried out by adding excess NaOCl to the tank, which was left for at least 48 hours. Tests were then made on samples of water for free chlorine, and any excess was neutralized by addition of $Na_2S_2O_3$.

In some battery-jar experiments, water from Holes Bay was filtered through Whatman No. 1 filter paper, and then sterilized by heating to 70°C. A control was run with Plymouth seawater treated in the same way. Later, water was used which had been only filtered, *i.e.* not sterilized (cf. Table 1).

In all experiments inorganic phosphorus and nitrogen salts were added to the medium before inoculation. They were added as $Na_2HPO_4 \cdot 12H_2O$, and either as $NaNO_3$ or $(NH_4)_2SO_4$ in concentrations to give 0.4 mg P/L and 3.0 mg N/L. In later experiments these additions of nitrogen and phosphorus were repeated twice weekly and even daily (cf. Table 1). Salts were always dissolved in a small quantity of distilled water before addition.

The inoculation was made from a laboratory culture of *Phaeodactylum*, not bacterial free, in the exponential phase of growth. The volume of culture added to the medium was such as to give approximately 200 cells/mm^3.

In the battery jar experiments the inorganic phosphorus content of the water was determined on samples of culture taken twice weekly, after thorough stirring, and before the next additions of N and P salts were made.

The samples for phosphate analysis were first filtered through a sintered glass funnel. Fifty-cc samples were taken for analysis by the Deniges reaction in Hehner tubes. The method of Hansen and Robinson (1953) was followed for concentration and quantities of reagents. In the later series of experiments these analyses were duplicated on an EEL absorptiometer using a slight modification of Harvey's method.

Growth rate and crop have been estimated by the increase in cell numbers. Cell concentrations were estimated on aliquots of the samples by haemocytometer counts, five to ten counts being made on each sample. It is probable that this method does not always provide an accurate estimate of the production of organic matter. In the present experiments, for example, it was noticed that cell size tended to decrease as an experiment progressed. Other methods have been used to estimate organic production (cf. Ryther 1956b). Spencer (1954) used the optical density of cultures, and measured the increase in absorption of light. However, the amount of pigment in the cell, as Spencer himself pointed out, varies under different culture conditions. Extractions of chlorophyll have also been used for productivity measurements, but the same objection may be raised, and there is the added complication of the varying amount of chlorophyll extracted by different solvents. On the industrial *Chlorella* plant, productivity has been measured by dry weight of the crop, and in the present investigations an attempt has been made in the last series to

TABLE 1. *Summary of main series of experiments (Series I to VII)*
Special culture conditions are indicated in addition to general procedure as described under Methods

Series	Date	Tank no.	Special conditions
I	13 Dec. 54 to 5 June 55	1	Chlorine sterilization. Culture volume 1,200 L, restricted to bottom of tank.
II	25 Mar. 55 to 30 Apr. 55	5	Seawater filtered only. Culture volume 1,200 L, restricted to top of tank.
		6	Seawater filtered only. Full tank volume (2,400 L).
		Battery jar no.	
III	19 Dec. 55 to 23 Jan. 56	1 to 4	In artificially lighted tank.
		5 to 8	In unlighted tank.
		1, 2, 5, 6	Chlorine sterilization.
		3, 4, 7, 8	Heat sterilization.
IV	17 Apr. 56 to 10 May 56	All (1 to 8)	Carbon dioxide addition.
		1 to 4	In artificially lighted tank.
		5 to 8	In unlighted tank.
		1, 2, 5, 6	Heat sterilization
		3, 4, 7, 8	Chlorine sterilization.
		1, 2, 5, 6	Additions of N (3 mg/L) and P (0.4 mg/L) during experiment (see Fig. 1).
V	29 May 56 to 25 June 56	All (1 to 8)	In unlighted tanks. Heat sterilization.
		1, 5	Semi-weekly additions of N and P.
		2, 6	Semi-weekly additions of N and P. CO_2 addition.
		4, 8	CO_2 addition.
VI	5 July 56 to 18 July 56	All (1 to 8)	On Generating Station roof. CO_2 addition. Double initial P concentration (0.8 mg/L). Semi-weekly additions of N and P.
		1, 2, 5, 6	Heat sterilization.
		3, 4, 7, 8	Seawater filtered only.
VII	14 Aug. 56 to 7 Sept. 56	All (1 to 8)	On Generating Station roof. CO_2 addition.
		1, 5	Heat sterilization.
		2, 3, 4, 6, 7, 8	Seawater filtered only.
		1, 4, 5, 8	Semi-weekly additions of N and P.
		2, 6	Daily additions of N and P.
		3, 7	Daily additions of N and P, and Mn, Fe, and E.D.T.A.

determine dry weight of crop, but this method is too lengthy and complicated for regular estimation.

RESULTS

1. *Tank and battery jar experiments without the addition of carbon dioxide*

Experiments were carried out both with large tanks (Table 1, Series I and II) and with battery jars (Table 1, Series III) in which, though N and P fertilizers were employed, no CO_2 was added to the cultures.

The results of the tank experiments (Series I and II) indicated, not unexpectedly, that the rate of increase of *Phaeodactylum* varied with the light conditions. The rate of division in January (1955) when light was almost minimal was about 1 division in 15 to 18 days (Table 2). In March/April, with increased daylight, the division rate over the exponential phase was 1 division in just over 6 days (Table 2, Series I) and in June, when light both in duration and intensity was roughly at its maximum, Tank 1 showed the highest division rate for all tank experiments—1 division in just under 2 days.

In Series I, Tank 1 was only half filled with culture (ca. 50 cm depth), and the comparatively low division rate in spring may have been partly due to loss of light reflected from the roof of the tank and to absorption by the upper walls. In a new series conducted in spring (Table 1, Series II) the culture in Tank 5 was restricted by means of a polythene bag to the upper 50

TABLE 2. *Rate of growth and peak populations of* Phaeodactylum *in tank experiments*

Series no.	Tank no.	Month	Temperature range °C	Maximum pH	Max. growth rate (division time in days)	Peak population (cells/mm³)	Period from inoculation for P to drop to 0.01 mg/L
I	1	Dec./Jan.	3–10	9.5	15–18	1200	38 days
I	1	early Mar./ Apr.	3–15	9.6	6	3500	—*
II	6	late Mar./Apr	10–20	9.6	3	1300	ca. 12 days

* Data for Series I, Tank 1, (March/April) refer to the second outburst of growth. The tank did not receive fresh inoculation or additional nutrients; no P figure can be given therefore.

cm. The rate of division in this culture was approximately twice as great—1 division in 3 days. A similar rate was also obtained for a full tank (Tank 6, Table 2), but only for a very short period during which the tank was left undisturbed so that strong stratification existed.

It is possible that total light variation was also mainly responsible for the differences in final levels of *Phaeodactylum* population. Beginning with an inoculation of 100 to 200 cells/mm³, in January, for example, a peak of ca. 1,200 cells/mm³ was reached, as compared with nearly 3,500/mm³ in March/April (Series I, Table 2).

Of factors other than light intensity which may have affected division rate in the tank experiments, temperature is known to have an accelerating effect up to 20°C (Barker 1935, Spencer 1954). Spencer found a particularly marked effect between 10° and 15°C. In early June, when the division rate of *Phaeodactylum* was at its highest, the temperature was ca. 15°C, whereas in the latter half of April it was around 10°C. However, in March during the second outburst of *Phaeodactylum* growth (Series I, Tank 1) with a division rate of 1 in 6 days, the mean temperature was 5°C, which is similar to that in January (6°) when the division rate was 1 division in 15 to 18 days (Table 2). The effect of temperature would thus appear to be slight, and any positive effect on photosynthetic rate appears to hold only at relatively high light intensities (cf. Harvey 1955). Moreover, since temperature affects respiration and photosynthesis, its effect on production is likely to be small.

In the majority of experiments where the seawater after filtration had been sterilized by chlorination, there was an initial lag in growth, amounting to as much as two weeks in tank experiments, and to about one week in battery jar experiments. It appeared possible that although no free chlorine was detectable at inoculation by chemical methods, minute traces might have been present, sufficiently toxic to *Phaeodactylum* cells to delay their growth. Alternatively, chlorine treatment may have lowered the concentration of some essential organic constituent. Tanks 5 and 6, Series II, were the only large-scale tank experiments where chlorination was not used, and it was significant that no lag in growth was observed. A preliminary test was made, therefore, on the battery-jar scale of chlorine sterilization against heat sterilization (Table 1, Series III). The results were not conclusive, as in most of the experiments at least a week's delay occurred before the exponential phase of growth; the lag appeared to have been due in part to some contamination. Later a more carefully controlled series of experiments (Table 1, Series IV) was conducted. Four jars with heat-sterilized water (Jars 1, 2, 5, 6, Table 1) all showed an immediate and rapid cell growth. Jars 3, 4, 7, 8, with chlorine sterilization, exhibited no growth for a week or more, after which satisfactory growth followed in three of the jars. It appeared, therefore, that the lag occurred only with chlorine treatment, and chlorination was not employed in subsequent series.

Although several series gave successful growth of *Phaeodactylum* all experiments tended to show a rapid fall in cell numbers after a peak population had been attained. Among the many factors possibly responsible (*e.g.* nutrient depletion, high pH), the reduction in light reaching the lower layers due to the density of the culture itself was first considered.

Measurements in March to May showed the compensation depth over a 24-hour period to vary from about 50 to 90 cm. At that depth only ca. 5% of the incident daylight remained. This illumination approxi-

mated to about 20 kilolux hours over the day. When, however, 1,200 cells/mm³ were also present in the tank water, at 1 cm from the surface only 50% of the surface light remained, and at 50 cm depth only 0.2% to 0.3% surface light. Since surface light had already been reduced to one-third of incident daylight by the tank covers, the illumination at 1 cm corresponded to 82 kilolux hours and at 50 cm depth to only 0.5 kilolux hours for the 24-hour period. From this it may be suggested that the compensation depth then lay at ca. 10 to 15 cm, if 20 kilolux hours per 24 hours be regarded as an average figure for compensation depth illumination.

When, after the decline of this culture, only 30 cells/mm³ were present in the tank, a further set of photometric readings was made. At this cell density the illumination at a depth of 1 cm had roughly doubled (169 kilolux hours for a 24-hour period). The light absorption now was only in part due to cells still present in the culture; it partly resulted from detritus arising from the decomposition of the *Phaeodactylum*. At 50 cm depth the illumination had risen to 33 kilolux hours for a 24-hour period, so that the compensation depth had increased with the smaller cell density from ca. 10 to 15 cm to a little more than 50 cm.

No photometric measurements were made when the concentration of *Phaeodactylum* was very high, but it is clear that when there was an average density of more than 3,000 cells/mm³ in the large tanks (April, Series I), the compensation depth must have approached the surface very closely. This also occurred in mid-winter even without high cell densities; some measurements made in December in a tank without *Phaeodactylum* showed that just beneath the surface the total illumination over 24 hours amounted to only 5 kilolux hours, *i.e.* well below the compensation depth illumination. Tests showed that no effective photosynthesis occurred even right at the surface.

To increase the light in the tanks, one 100-Watt lamp was placed some six inches from the surface of one of the large tanks which was only half filled with water (*i.e.* ca. 50 cm depth). Directly underneath the bulb the illumination at the surface gave some 73 kilolux hours extra over a 24-hour period. At the bottom of the tank the lamp supplied 30 kilolux hours if the light source was directly overhead. At the sides of the tank, however, the extra lighting amounted to 8 kilolux hours at the surface, and to only 3 or 4 kilolux hours at the bottom. To increase the total lighting in the tank experiments still further, therefore, four lamps were used, each 100 Watts. The use of more than four bulbs was inadvisable as the continuous burning of even the four lamps caused a rise in temperature in the tanks of 4°C.

The effect of this increased illumination was tested in Series III (Table 1). Battery jars 1 to 4 were placed inside an artificially lighted large concrete tank, and the growth rate of the cultures compared against controls (Jars 5 to 8) placed in an unlighted tank (*i.e.* receiving daylight only). The artificially illuminated jars gave a division rate of 1 in ca. 3–4 days as compared with 1 division in 5–6 days for the controls. However, the final densities obtained were similar in both tanks, and growth soon levelled off (Table 3).

Of factors other than light which may have caused a slowing of cell multiplication, rise in pH was probably the most significant. Spencer (1954) has shown that when the pH of a *Phaeodactylum* culture exceeds about 8.6 the growth rate declines; *Phaeodactylum* cells will continue division even at a very high pH (9 to 10) but a retardation of divi-

TABLE 3. *Rate of growth and peak populations of* Phaeodactylum *in battery jar cultures*

Series no.	Jar no.	Inoculation date	Temperature range °C	Max. growth rate (division time)	Peak population (cells/mm³)	Period from inoculation for P to drop to 0.01 mg/I
III	2–4	30 Dec. 55	7 –11.5	3–4 days*	2400–3700	—
III	5–8	30 Dec. 55	2.5–8.5	5–6 days	3300–4800	—
IV	1–2	17 Apr. 56	11.5–18	2 days*	6100–7000	9 days
IV	5–6	17 Apr. 56	9 –16	3 days	4700–8500	10 days
V	1–4	29 May 56	13.5–18.5	ca. 24 hrs.	3700–9900	9 days
V	5–7	29 May 56	13.5–18.5	36–48 hrs.	3000–6600	—
V	8	29 May 56	13.5–18	ca. 24 hrs.	5700	—
VI	1–8	5 July 56	13.5–20	<24 hrs.	5500–18000	<4 days†
VII	1–8	14 Aug. 56	11.5–19	30 hrs.	10300–32000	>3 days

* Additional artificial illumination.

† Double initial P concentration (0.8 mg/L); >0.4 mg absorbed in 4 days.

sion occurs which becomes more marked as the pH rises.

In those cultures which showed a lag in cell division, the changes in pH were slight initially. In Series I, for example, the pH changed little from about 8.0 to 8.2 until more than 14 days had elapsed. However, the pH then rose rapidly to exceed 9.0 with the rapid cell multiplication. Generally, in both tank and battery jar experiments the pH rose rapidly to more than 9 during the exponential growth phase, but when the fall in cell population occurred, especially in the tank experiments, pH changes did not follow immediately. For example, in Series I, Tank 1, the pH which had risen to about 9.5 at the peak population remained at over 9 for almost three weeks after the culture had declined. Similarly Tank 6, Series II, at its peak density in mid-April of 1,300 cells/mm^3 reached pH 9.6 (cf. Table 2); the pH remained virtually unchanged for another fortnight although the *Phaeodactylum* had meanwhile declined to less than 100 cells/mm^3. Probably effective stirring of the tanks would have increased growth by reducing the pH, but it was decided that use of CO_2 would be a better method. It was, therefore, decided to run a series of experiments in which "pure" CO_2 (cf. p. 121) was added in an attempt to maintain the pH below 9. Owing to the amount of CO_2 required, all experiments were limited to battery jars (cf. Table 1, Series IV, V, VI, VII).

2. *Battery-jar experiments with the addition of CO_2*

In the first series of experiments in which CO_2 was employed (Table 1, Series IV) photosynthesis raised the pH of cultures to between 9 and 10 in nine days. At this stage CO_2 was added to some jars and the pH fell rapidly. CO_2 was used directly from cylinders in these early experiments, and was not diluted with air, so that a few minutes of carbonation was sufficient to reduce pH. After CO_2 application ceased, however, the pH climbed comparatively rapidly. For example, Jar 1 showed a pH of 9.5 on 30 April. This was reduced with a few minutes of CO_2 addition, and the following morning the pH was 8.45. Twenty-two hours later the pH had risen to 8.9, and in another 48 hours it had reached its former value of 9.5. Similarly Jar 6 was reduced with carbonation from pH 9.2 to 7.9 on the morning of 1 May. Twenty-two hours later the pH had reached 8.6, and in another 48 hours had climbed to approximately its former value (9.3).

It was clear from the results of Series IV that addition of CO_2 was beneficial. The growth rates were comparatively high in the experiments—ca. 1 division in 2 days for jars receiving additional artificial lighting and 1 division in 3 days for jars receiving natural daylight only (Table 3). The peak densities achieved were also higher than those which had been reached before; densities of the order of 5,000 cells/mm^3 for artificially lighted jars, and ca. 4,000 cells/mm^3 for daylight jars were established in a fortnight. Thereafter, however, the rate of growth in all jars tended to decline, although one culture (Jar 6) continued to increase for ca. 20 days reaching a density of 8,500 cells/mm^3 (Table 3).

It was possible that more constant and continuous growth of *Phaeodactylum* might have resulted had the pH been more carefully adjusted between 8.0 and 8.5. In Series V, and especially VI and VII (Table 1), more continuous carbonation was attempted after the first week, when the pH had risen to between 9 and 10. In practice, however, it proved very difficult to adjust pH without apparatus specifically for regulation: the pH fell sharply with CO_2 addition, but as soon as carbonation was stopped the pH soared. For example, in one culture (Series VI) CO_2 reduced the pH from 9.8 to 8.1 and in less than 24 hours after cessation of carbonation the pH had returned to 9. Another remarkable example was the reduction of pH to 6.3 with CO_2 and its return to 8.8 in just under 24 hours. In a later experiment (Jar 1, Series VII) the pH was accidentally reduced to 5.8, but the culture still grew successfully and the pH rapidly soared to between pH 8 and 9. Many other instances of wide fluctuations in pH, even as low as pH 5 (Jar 7, Series VI) and as high as pH 10 occurred, but in no case was

Phaeodactylum killed. Indeed photosynthesis caused a rapid climb from low pH levels. While it is true that extreme pH values, especially at high levels, may have reduced the rate of growth temporarily, in no case were they responsible for cessation of growth.

In Series IV phosphate concentrations showed a remarkable drop correlated with the rapid increase in cell population. In two artificially lighted jars (Jars 1 and 2) less than 0.1 mg P/L was reached after 6 days, and 3 days later the amount of P was undetectable (less than 0.005 mg P/L) (Table 3). In two jars (Jars 5 and 6) receiving only natural illumination the rate of cell division was slightly lower and P uptake was somewhat slower over the first 6 days. However, after a further 3 to 4 days none was detectable (Fig. 1). It was decided that with this high uptake, extra nutrients were desirable, and two further additions of N and P (each 0.4 mg P/L and 3 mg N/L) were made subsequently to Jars 1, 2, 5, and 6. Phosphate alone was followed and showed again very rapid uptake, so that even 3 days after a further addition of nutrient, very little P could be detected. After the first few days P was almost continuously below 0.1 mg/L (Fig. 1), despite the additions, which amounted to a total of 1.2 mg P/L.

Similar P changes were repeated in those jars which showed the initial lag in *Phaeodactylum* growth (owing to chlorine sterilization), but only after 7 to 10 days (Fig. 1) during which time very little change in P occurred. The marked changes correspond to the time when the *Phaeodactylum* began to grow rapidly.

This high uptake of P, as a result of which less than 0.01 mg P/L remained after little more than a week in dense cultures using CO_2, suggested that repeated additions of nutrients might prolong the exponential phase of growth in cultures. Ketchum (1939a) has shown that P becomes a limiting factor in dense *Nitzschia* (= *Phaeodactylum*[1]) cultures when the concentration falls below ca. 0.016 mg P/L.

The results of Series V, VI, and VII in which, in addition to CO_2, repeated applications of nutrients were made clearly suggested increased growth of *Phaeodactylum* with higher final populations (Table 3). However, although phosphate was taken up very rapidly, growth of the alga still declined at least slightly after a comparatively short period. For example, in Series V, after some 10 to 14 days the rapid growth in all cultures declined somewhat, although those cultures which were receiving semi-weekly additions of N and P as well as CO_2 (cf. Table 1) showed considerably higher rates of growth as compared with those that had either only extra N and P, or only extra CO_2. It is true, however, that those cultures which received only one addition of N and P initially, but which had CO_2 added to regulate pH, showed a rather better rate of growth than those which had N and P added repeatedly but had no extra CO_2. It seems, therefore, that although P was taken up by the algae in relatively great quantities, it was not efficiently utilized when the carbon source was in lowered concentration. Uptake of phosphate by P-deficient cells is reported by Scott (1945) for *Chlorella*, by Rice (1953) for *Nitzschia closterium* (= *Phaeodactylum*), and by Armstrong (reported by Harvey 1955) for *Phaeodactylum*. The marked P uptake is seen in Series V: some jars had 0.4 mg/L added every 3 to 4 days, so that 3.6 mg P/L had been added by the end of the experiment, but after the first 10 to 14 days never more than 0.01 mg/L was recorded while the culture maintained a high density.

Series VI had an unusually high initial P concentration—ca. 0.8 mg/L (Table 1). The rapid uptake of nutrients, however, was equally marked in this Series: less than half the phosphate remained after 4 days (Table 3), during which time the *Phaeodactylum* was growing very actively, and a week after inoculation, despite a further addition of nutrients, of four jars tested all showed concentrations below 0.02 mg P/L.

In Series VII, also, phosphate was reduced

[1] It is probable that the alga was *Phaeodactylum* since it appears that the stock was derived from Plymouth cultures.

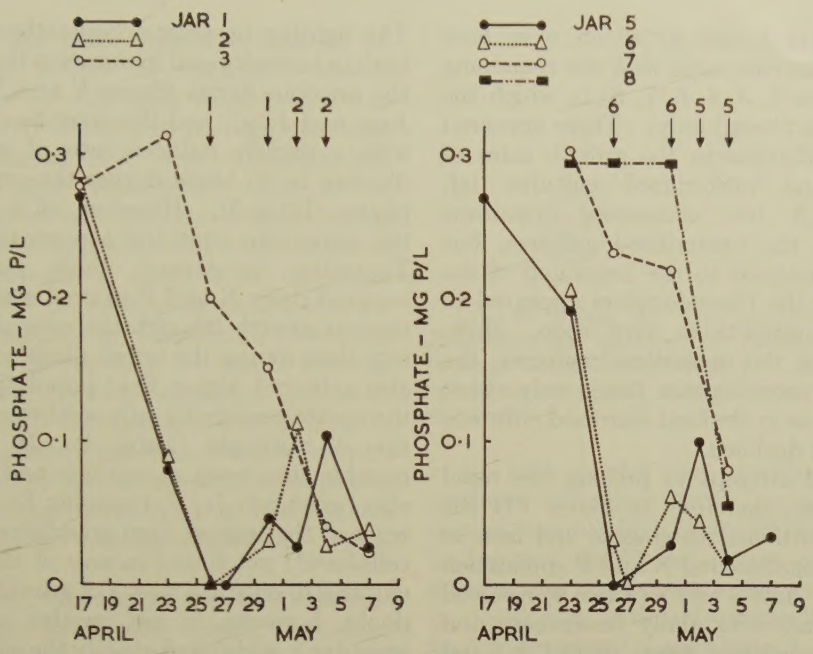

FIG. 1. Changes in phosphate-P in battery-jar experiments (Series IV). Jars 1–3 were artificially lighted; Jars 5–8 received daylight only. Jar 4 is omitted as no growth occurred in this culture. Arrows indicate dates of further additions of P (0.4 mg/L) to certain jars shown by numbers attached to arrows. Jars 3, 7, 8, were chlorine sterilized; a lag occurred before P was rapidly utilized. (No P concentrations recorded for Jars 6, 7, 8, on 17 April, but same amount of P added initially to all jars.)

to approximately one-tenth of its value only 3 days from inoculation. In the course of three weeks 7.6 mg P/L were added, but never more than 0.1 mg/L was detected. Usually concentrations up to 0.06 mg P/L were recorded, but nil values were obtained from some cultures. In the same Series, however, at the very end of the experiment, an indication of regeneration of P in a declining culture was noticed. In Jar 1 during the last 3 days the number of cells showed a slight decline, and on the last day of the experiment the amount of P reached nearly 0.8 mg/L as opposed to values of less than 0.01 mg/L for the previous three weeks. Over the same period Jar 2 showed a tremendous drop in vigor; the number of healthy cells fell in 2 to 3 days from ca. 17,000 to only 2,000/mm^3. As the cell density fell, phosphate, which had been very low for the whole of the experiment, increased rapidly to 1.7 mg P/L, and the pH fell from 8.9 to 6.9 which might suggest marked bacterial activity.

Some continuation of cell growth resulted in those cultures where repeated additions of N and P and of CO_2 were made and the final populations were also greater (Table 3, Series V and VI). In Series V, for example, densities of about 10,000 cells/mm^3 were attained, and in Series VI, on the roof of the Generating Station with increased natural lighting, distinctly higher peak populations varying from 11,000 to 18,000 cells/mm^3 resulted, this growth being achieved in only about 11 days. The division rate was also high in the latter Series over the exponential phase (1 division in less than 24 hours—Table 3). However, this phase lasted for only 7–8 days and thereafter the division rate fell to ca. 1 division in 6 days, despite continued additions of N, P, and CO_2.

Heat sterilization was employed for all cultures in Series V and VI (cf. Table 1). It was possible that this treatment might have reduced the concentration of some essential factor thus slowing growth. Therefore in Series VII the growth of two

cultures (Jars 1 and 5) which were heat sterilized, was compared with the remaining cultures (Jars 2, 3, 4, 6, 7, 8) in which the seawater was filtered only. There appeared to be no difference in the growth rates of sterilized and unsterilized cultures (cf. Table 4). A few competing organisms occurred in the unsterilized cultures, but they were confined to the beginning of the experiment; the *Phaeodactylum* appeared to crowd out competitors very soon. However, even in the unsterilized cultures, the exponential growth phase lasted only about a week and, as in the heat sterilized cultures, growth then declined.

As a final attempt to prolong the rapid growth phase, therefore, in Series VII the effect of additional manganese and iron as well as carbonation and N and P application was tested. Jars 3 and 7 (Table 4) received after the first week daily manganese and iron with a chelating agent (E.D.T.A.) and N, P, and CO_2. Since phosphate was so rapidly absorbed in dense cultures receiving CO_2, some experiments were also conducted (Series VII, Table 1) in which, after the first week of growth, the effect of daily additions of N and P was tested against semi-weekly additions (cf. Table 4).

Series VII was run on the roof of the Power Station without artificial lighting.

TABLE 4. *Series VII: changes in* Phaeodactylum *population in various jar cultures (cells/mm³)*

Note the marked reduction in *Phaeodactylum* with *Monas* infection in Jars 4, 5, and 8.

	Jar culture number							
	1	5	2	6	3	7	4	8
Nutrient addition after 1st week	Twice weekly N + P (heat sterilized water)		Daily N + P		Daily N + P + Mn + Fe + E.D.T.A.		Twice weekly N + P	
14 Aug. (inoculation)	202	214	228	232	210	212	202	240
17 Aug.	870	878	1316	1346	1194	1406	1092	1442
20 Aug.	3770	3908	4770	5838	4614	5318	5460	5588
23 Aug.	8647	9856	11048	13504	11304	13144	10256	11072
27 Aug.	13808	16000	15088	18984	10696	16492	5712*	2990†
30 Aug.	16148	15720	15208	23840	15544	21450	3530*	6650
4 Sept.	17640	15984	17448	26508	20296	29492	6592	3800*
7 Sept.	16480	6152†	2202	25800	19408	31870	7736	1818*

* Heavy *Monas* infection.

† Reduction due to harvesting crop.

The lighting in August/September was less both in intensity and in duration than during the previous Series (Series V and VI run in June and July), and this may be correlated with a slightly reduced rate of growth (1 division in 30 hours during the exponential phase—Table 3). However, all 8 jars gave the same rate over the exponential phase. Thereafter, in general, those jars which received daily N and P showed a more continuous growth (though this was at a lower rate than during the initial phase), and they also achieved higher final populations than the controls receiving only semi-weekly addition of nutrients (Table 4). It appeared possible that extra manganese and iron was also beneficial: Jar 7, receiving Fe and Mn, reached the highest final population (32,000 cells/mm³) yet found in any of these mass cultures in only 3½ weeks of growth. Some doubt, however, is cast on this conclusion since Jar 3, which had exactly the same treatment as Jar 7, did not show increased population or accelerated rate of growth over a culture (Jar 6) which received daily N and P but no additional Mn and Fe (Table 4). Further experiments are necessary to demonstrate clearly the effect of extra manganese and iron.

The high algal densities in Series VII allowed a preliminary attempt at harvesting cultures. Fourteen liters of culture from Jar 8, Series VII, with a population of 14,000 cells/mm³ were filtered and yielded approximately 4 g (wet weight) of algal matter. Jar 7, with a much richer *Phaeodactylum* culture (ca. 28,000 cells/mm³) was also harvested: 13.4 liters yielded ca. 9.4 g (wet weight), which after some washing and drying gave 4.05 g (It is not certain that all the salts had been washed from the cell mass.); 3.83 g of this dry material when ashed was reduced to 0.74 g. Thus the original 4.05 g would give 3.27 g of organic matter + 0.78 g ash, *i.e.*, ca. 81% organic matter.

3. *The adverse effects of a flagellate infection on growth*

Sterilization by means of the addition of chlorine to the large-scale tank cultures has been shown to be ineffective in ridding the

culture of all other plankton species, although the variety of competitor species which grew in the tank experiments was comparatively small and the densities generally remained low. One flagellate has, however, been repeatedly observed in *Phaeodactylum* cultures; the contaminating organism has been identified with the genus *Monas* (Ehrenberg) Stein. The organism varies in size depending on the food available. In actively growing culture the body length is 8 to 10μ and the width 4 to 8μ. The length of the long flagellum is just under 30μ and that of the short one 4 to 5μ (Fig. 2). As yet no attempt has been made to identify the monad to species since it is hoped to investigate the morphology in bacteria-free cultures under varying nutritional conditions.

In Series I the monad was first observed in December 1954, only a week or so from inoculation, but in small numbers. On 27 January 1955, when *Phaeodactylum* was growing actively, numbers of *Monas* were still low (ca. 10 cells/mm^3) but by 10 February the monad had risen sharply to 170 cells/mm^3. This rise partnered a rapid fall in *Phaeodactylum* from 1,200 to 88 cells/mm^3, and afterwards the flagellate also declined. A similar cycle occurred during March/April (Series I, Tank 1). During the second outburst of growth of *Phaeodactylum* very few monads were present, but as the *Phaeodactylum* dropped very sharply from its peak value, the flagellate population increased. Following the reduction of the *Phaeodactylum* culture to a very low density, the monad population fell also.

Other tank experiments gave similar results. Thus Tank 6, Series II, beginning with an inoculation of some 100 *Phaeodactylum* cells/mm^3 on 25 March, showed a marked growth to a density of some 1,300 *Phaeodactylum*/mm^3 on 6 April, and during that time the monad was not recorded. On 15 April the upper tank layers showed a slight increase in *Phaeodactylum* (1,500 cells/mm^3) whereas the bottom layers had shown a sharp decline (less than 200 cells/mm^3). Coincident with this *Monas* had appeared; more than 200/mm^3 were present. A few days later both top and bottom layers

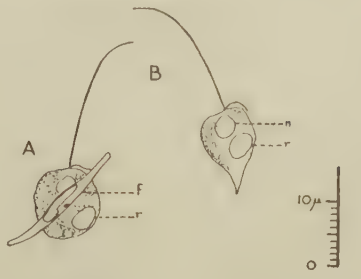

FIG. 2. *Monas* sp. Two individuals from a *Phaeodactylum* culture. *A.* specimen actively feeding; *B.* unfed individual; *f* = *Phaeodactylum* cell being consumed; *n* = nucleus; *r* = reserve substance.

in the tank showed very low *Phaeodactylum* densities with many empty frustules, but the monad was still high (230 cells/mm^3). Following this, the *Phaeodactylum* continued to decline, and the flagellate also showed a fall in population until only some 18 monads/mm^3 were present a week later.

It would appear that *Monas* does not flourish in culture when *Phaeodactylum* is in a rapid state of growth, but after a heavy density of *Phaeodactylum* has been established and the exponential phase is past, the monad can show a very sudden outburst of multiplication, and the *Phaeodactylum* culture is rapidly reduced.

This rapid reduction by *Monas* was also very common in battery-jar experiments. Thus all cultures in Series IV showed marked declines in population coinciding with large numbers of the monad. Jar 1, for example, fell in three days from 6,000 *Phaeodactylum* to under 1,000 cells/mm^3, and over the same period the monad rose to 500 flagellates/mm^3. In Series V, Jar 6 fell in four days from over 6,000 *Phaeodactylum* cells/mm^3 to under 500, and Jar 2 in three days from 10,000 to 2,400 *Phaeodactylum*/mm^3; both declines coincided with the development of the flagellate population. In Series VI, Jar 5 showed a fall from over 5,000 to 500 *Phaeodactylum*/mm^3 in only two days, when the monad appeared in large numbers. On the other hand, in Jars 4, 6, 7, and 8 in the same series, the flagellate infection remained light with fewer than 100 flagellates/mm^3, and in these jars the *Phaeodactylum* continued to increase in density.

Figure 3 shows a scatter of points obtained

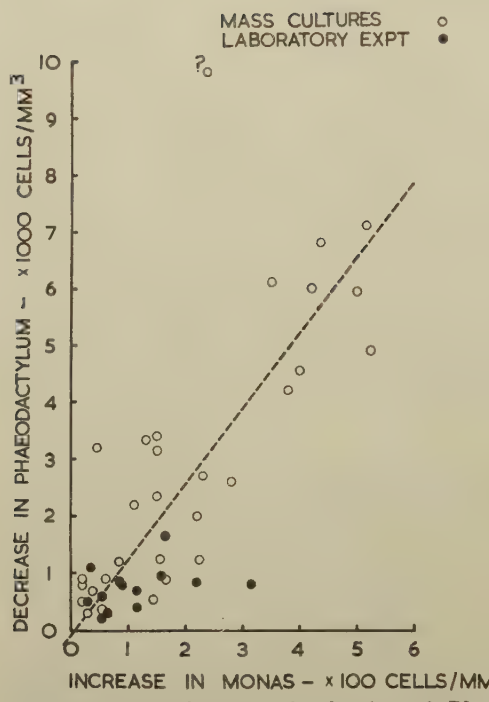

FIG. 3. The decreases in density of *Phaeodactylum* and corresponding increases in *Monas* sp. in mass cultures (tank and battery-jar experiments) and in laboratory experiments. The dashed line represents the relationship 1,000 *Phaeodactylum* decrease per 100 *Monas* increase. (? = Jar 2, Series VII, where a marked fall in *Phaeodactylum* was accompanied by a rise in bacteria and flagellates but not *Monas*.)

by plotting the decrease in cell numbers of *Phaeodactylum* cultures against the corresponding increase in *Monas* over the same period. The length of time involved varies for each point. The points were obtained from both tank and battery-jar experiments in Series I, II, IV, V, VI, and VII. A few laboratory experiments were also carried out on the reduction of *Phaeodactylum* populations by known concentrations of *Monas*. These few results are included on Figure 3.

The positive correlation obtained is good, especially since conditions in the different cultures varied a great deal, and might in some cases have been more favorable to the growth of *Phaeodactylum* so that the population increased at a faster rate than it was being affected by the monad. The anomalous position of the point obtained for one culture (Jar 2, Series VII) may be explained if either the *Phaeodactylum* was dying back due to factors other than the presence of the monad, or if growth of the flagellate was limited by factors other than those resulting from the decline of the alga.

Figure 3 suggests that the average decrease in *Phaeodactylum* per increase of 100 *Monas* was ca. 1,000/1,200 cells. However, it is not possible to say whether the effect of the flagellate upon the alga is a direct one, since neither the experiments in tanks and jars nor those in the laboratory were performed with bacteria-free cultures.

The monad has been kept in a bacterial culture grown in sucrose and glucose solutions, and in these cultures appeared as a bacterial feeder; thus it is possible that the *Phaeodactylum* was first attacked by bacteria, and that the flagellate then fed on the bacteria. It was observed, however, that in many cases the flagellate actually engulfed *Phaeodactylum* cells. There is no doubt that *Monas* can feed on cells other than bacteria; it has been kept, for example, in a culture of bakers' yeast on which it feeds and grows readily. Thus it is possible that to some extent *Monas* had a more direct grazing effect on the *Phaeodactylum* population.

Examination of aged *Phaeodactylum* cultures showed many empty frustules suggesting grazing by *Monas*, but if a direct feeding effect does operate, a very large grazing fraction must be removed when the monad commences full multiplication. On the other hand, a considerable number of the algal cells in old *Phaeodactylum* cultures have been observed lying on the bottom with protoplasmic contents intact. This suggests that the flagellate might have some toxic effect on the alga, as well as feeding upon it.

Various laboratory experiments were carried out to determine the effect of old and of actively growing algal cultures on the flagellate. Figure 4 shows the effect on a monad population of successive additions of an aged *Phaeodactylum* culture which was showing very little change in cell concentration. With each addition of aged *Phaedactylum* culture there was an increase in the monad population during the following 2 to 3 days which corresponded to a decrease in

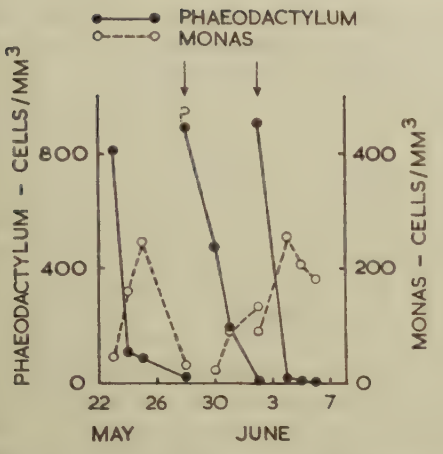

FIG. 4. Decline of an aged *Phaeodactylum* laboratory culture when added to a *Monas* laboratory culture. The *Monas* population shows a corresponding increase and a decline later. On two dates, shown by arrows, further addition of aged *Phaeodactylum* was made; the same effects followed. (? = *Phaeodactylum* density estimated from volume of culture added.)

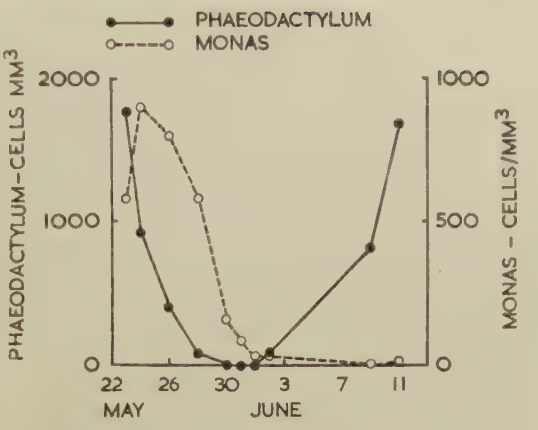

FIG. 5. Decline in an aged *Phaeodactylum* laboratory culture when added to a *Monas* laboratory culture. The *Monas* increased to a maximum but then fell. After the decline of *Monas* the *Phaeodactylum* entered a new rapid growth phase and the *Monas* remained low in density.

the *Phaeodactylum* population of ca. 1,000 cells/mm³. After each rise in *Monas* population, the density of the flagellates decreased again to rise once more after the next addition of old *Phaeodactylum* culture (Fig. 4).

On the other hand, from experiments where *Phaeodactylum* cultures in the exponential growth phase were added to flagellate cultures, it appeared as from the observations in the tanks and jars, that the flagellate was not able to attack effectively algal cells in rapid growth. One such experiment (Fig. 5) shows the effect of the monad on an old *Phaeodactylum* population similar to what had been repeatedly observed before. This culture, however, was thereafter left without further additions of *Phaeodactylum* and after the algal population had been reduced to very low densities for four days, it began to increase again. The rate of increase became very high (1 division in 24 hours) and a clear exponential phase of growth developed. Over this same time *Monas* decreased to a very low concentration (Fig. 5).

The results of tank (Tank 1, Series I) and jar experiments also suggest that a culture infected with *Monas* may survive the infection, and after the decline in monad density *Phaeodactylum* may recover. In Series VII, Jar 4, the population of *Phaeodactylum* fell with a heavy infection of monads from 10,000 to 3,500 cells/mm³ in a matter of a week (cf. Table 4). After a further week, however, 7,700 cells/mm³ were present, and the pH, which had been low, was rising again, suggesting strong photosynthetic activity.

What causes the flagellate to remain sparse while the alga is growing steadily is uncertain. Physical factors may be involved, but it is unlikely that either temperature or pH is important in this consideration, since *Monas* appears to have as wide a tolerance as *Phaeodactylum*.

Possibly some other organisms as well as the particular monad under discussion may prove to have a deleterious effect on *Phaeodactylum*. In the present experiments there is only one possible example. In Series VII, Jar 2, a reduction from more than 17,000 to some 2,000 cells/mm³ occurred in a matter of three days (Table 4): a further 16,000 cells/mm³ were observed to be present but all in unhealthy condition. The decline in vigor of this culture was not accompanied by any marked appearance of *Monas* but it was associated with a heavy growth of unidentified dinoflagellates and bacteria.

DISCUSSION

The results show that it has been possible to grow comparatively dense mass cultures of *Phaeodactylum* in volumes ranging from 15 liters to as much as 1,000/2,000 liters. The final densities achieved (cf. Tables 2 and 3) range from about 1,000 to 32,000 *Phaeodactylum*/mm^3. The use of chlorine as a tank sterilizing agent has been shown to be deleterious; heat was satisfactory, but it was possible to establish fairly pure cultures of *Phaeodactylum* in seawater that had been filtered only.

Even when sterilization methods were used, invading organisms (especially flagellates and ciliates) were found from time to time both in large-scale tank cultures and in the jars. All experiments were carried out in the open, close to the sea, and tanks were only loosely covered. These experiments thus differed considerably from laboratory cultures, and the possibility of infection, even after inoculation, was high. However, the density and variety of invading organisms was small. The one exception was *Monas* sp., which has been shown to occur generally in cultures and which can become a marked predator.

Comparatively few large-scale experiments have been attempted using fertilizers with unsterilized seawater to grow large concentrations of phytoplankton. Edmondson and Edmondson (1947) and Pratt (1950) using concrete tanks at Woods Hole showed that a variety of organisms would grow in the tanks though there tended to be domination by one or two species. The maximum numbers found in these experiments were much lower than in the present study: Edmondson and Edmondson gave a maximum of ca. 4,000 cells/cc and Pratt 400,000/cc, *i.e.*, 4/mm^3 and 400/mm^3, respectively. Recent tank experiments at Woods Hole with zooplankton also present (Raymont and Miller unpublished) have shown two or three dominant phytoplankton species (*Nannochloris*, *Exuviella*, *Nitzschia*). Densities ranged up to 2,000 cells/mm^3.

In the present series of experiments the success of the *Phaeodactylum* may be attributed in part to the relatively high original inoculation (100 to 200 cells/mm^3). Nevertheless, the results indicate, in agreement with those of previous workers, that *Phaeodactylum* is a species which competes very successfully with others (with the exception of *Monas*) and it is thus very suitable for further mass culture work.

Results show that the growth rate of *Phaeodactylum* over the exponential phase varied considerably from one culture series to another (cf. Tables 2 and 3). The lowest rate (1 division in 15 to 18 days) occurred in mid-winter and the highest rate (1 division in 24 hours) in high summer. This maximum growth rate is only about half that recorded by Spencer (1954) with small-scale laboratory cultures with optimal light and temperature conditions. Ryther (1956a) has recently demonstrated the overriding importance of light in phytoplankton production, and there is little doubt that the varying growth rates in the present experiments are mainly correlated with light conditions (cf. Edmondson 1955). The maximum rate of 1 division in 24 hours with daylighting only was obtained in battery jars (Series V and VI in June/July); the fastest rate for larger-scale tank experiments for June was 1 division in 48 hours. In the laboratory, stock cultures during summer showed an initial division rate of 1 division in 18 hours. This rate, however, dropped off rapidly, and the more usual rate was 1 division in 24/36 hours. The maximum rates quoted for mass cultures in both battery jars and tanks may, therefore, be regarded as fairly satisfactory.

Although short-lived bursts of phytoplankton have been recorded from the open sea by many workers, in general there is very little production over winter (cf. Ryther 1956a). Somewhat better growths may occur in sheltered inshore waters (cf. Gross, Marshall, Orr, and Raymont 1947; Marshall and Orr 1948, for Loch Craiglin), but these are then associated with shallow depth and marked stability of the water column. It is, therefore, somewhat surprising that growth was obtained in January (Series I) especially when a rain of coal and dust particles on the tanks reduced the low incident light to a marked degree. Experiments in December showed indeed the com-

pensation depth right at the surface, and growth did not occur during that month. However, sufficient light penetrated by January to give a low rate of production in a stable shallow tank.

Undoubtedly even in spring light was a limiting factor in tank experiments. The compensation depth was at only 50 cm when a comparatively low cell population was present (30 cells/mm^3); with richer flowerings the compensation depth rapidly approached the surface. Steemann Nielsen (1952) has drawn attention to light as the final limiting factor in areas like Walvis Bay where relatively large amounts of nutrients occur naturally.

Present investigations suggest that for *Phaeodactylum* the illumination at the compensation depth approximated to 20 kilolux hours for the 24-hour period. Jenkin (1937), using *Coscinodiscus*, found over the summer a compensation depth in the English Channel of 45 m where the average energy flux was about 0.13 g-cal/hr/cm^2. Schreiber (1927), using artificial light, found the optimum value for *Biddulphia mobiliensis* to be 0.5 g-cal/hr/cm^2. Schomer and Juday (1935) for green algae in Wisconsin Lakes, found the energy flux to vary from 0.25 to 0.95 g-cal/hr/cm^2. The figure of 20 kilolux hours obtained in the present investigation corresponds approximately to 0.3 g-cal/hr/cm^2. The order of magnitude is well inside that found by various workers for other algae.

The high densities of *Phaeodactylum* in these experiments were obtained without addition of soil extract or other additional organic or inorganic nutrient apart from N and P. The few experiments that were carried out to test the effect of extra iron and manganese, which have been shown by many workers, particularly Harvey, to limit growth in some phytoplankton species suggested that these extra metallic ions produced somewhat richer cultures, although the results were not clear-cut. It appears that *Phaeodactylum* is an unexacting species in its nutritional requirements as suggested by Harvey (1955).

Apparently, however, *Phaeodactylum* must be acclimatized to some degree to different nutrient conditions. Thus in the earlier work the stock cultures were all grown with sodium nitrate as extra nitrogen source. When such cultures were used in mass culture using ammonium sulphate as extra nitrogen source, there was some delay before the cells took advantage of the additional nutrient. On the other hand, if cultures were grown in the laboratory with ammonium sulphate, they grew without any suggestion of lag in mass culture when this salt was used as fertilizer.

The high rate of growth corresponding to the exponential phase appeared to last in nearly all series for 10 to 14 days. In most experiments the peak population was followed by a very rapid fall in cell densities, and the fall was usually associated with the presence of *Monas* sp. in relatively high numbers (more than 200/mm^3). In other experiments the exponential phase was succeeded by a lower growth rate, but after about 3 weeks a plateau phase was reached. Only in a very few experiments (*e.g.*, Jar 7, Series VII; Jars 6 and 8, Series VI) was a fairly high rate of growth continued until the end of the experiment.

The differences in final level of population suggest that various factors became limiting. Series IV, V, VI, and VII strongly suggest that, apart from light, one of the chief limiting factors was high pH with lowering of CO_2 content. The use of "pure" CO_2 in these series of experiments clearly demonstrated an acceleration of growth rate, and in some cases the addition of CO_2 also led to some continuation of growth. This beneficial effect of CO_2 is important if, in the future, the mass culture of phytoplankton with the use of partially purified industrial gas effluent becomes feasible. For such mass culture the use of an unexacting species such as *Phaeodactylum* is obviously also important. The low silica content of the alga, in contrast to that of most diatoms (Harvey 1955 quotes a minimum of 1%), is a further recommendation.

It is clear that nutrients were absorbed very rapidly in these large-scale cultures (cf. Pratt 1949). Undoubtedly some of the earlier figures for P are somewhat artificially depressed, as it has been shown recently by

Wood, Lander, and Benstead (unpublished) that at high pH, phosphate in relatively high concentration tends to be precipitated, and the older method used for phosphate determinations gave figures at the upper range (ca. 0.4 mg P/L) which were somewhat low. But more recent phosphate tests have also shown that in those cultures which showed an immediate rise in cell population, approximately 0.4 mg P/L could be taken up in 4 to 10 days (Table 3). In those cultures where cell concentrations of many thousand *Phaeodactylum*/mm³ were present, repeated addition of P did not raise the general level very much (Fig. 1). In some experiments (Series V, VI, VII) although as much as 7 mg P/L were added, only a small fraction of inorganic phosphate could be detected at any time. Only in those cultures where a lag in cell multiplication occurred was phosphate not taken up rapidly, and even there as soon as the cells began to increase rapidly P changes followed the usual pattern (cf. Fig. 1). Edmondson (1955) suggests that addition of nutrients at first raises the photosynthetic rate and that population increase may not be so rapid; the maximum photosynthetic rate was not reached until 5 to 12 days after fertilization. In most of the present experiments, provided there was no lag due to chlorination, population increase followed fertilization immediately.

Observations on both the laboratory-scale and on mass cultures showed that one flagellate (*Monas* sp.) competed very successfully with *Phaeodactylum*. Although the flagellate was usually present in cultures, only at a certain stage in the growth of the *Phaeodactylum* where cell multiplication was slowing was the monad itself able to grow rapidly. It may be that either *Phaeodactylum* stops absorbing nutrients from the medium essential for the growth of the flagellate, or *Phaeodactylum* may release substances essential for the growth of the monad which are not present in sufficient concentration early on. *Monas* appears then to use up these essential substances, for after an outburst of reproduction it declines, and *Phaeodactylum* then enters a new cycle of rapid growth (cf. Fig. 5). The very rapid decline of *Phaeodactylum* cultures when *Monas* was abundant appears to be due partly to the alga being consumed, but there is some suggestion of a toxicity effect also.

Harvesting has been attempted in only one or two experiments. From Jar 7, Series VII, 13.4 liters of culture containing 28,000 *Phaeodactylum*/mm³ yielded 4.05 g of dry material with ca. 80 % organic matter. Then: $28{,}000 \times 13.4 \times 10^6$ cells = 4.05 g (dry weight). Therefore: 1×10^6 cells $= \frac{4.05}{28 \times 13.4}$ mg $=$ 0.0108 mg dry weight per million cells, of which ca. 0.0087 mg (80 %) is organic matter.

Various cultures of *Chlorella* have been analyzed for dry weight. The figures suggest that 1 g/L dry weight is obtained from cultures of density 1×10^5 to 3×10^5 cells/mm³ (Burlew 1953). Thus 1 million *Chlorella* cells would yield from 0.01 mg to 0.003 mg (dry weight). The upper figure is readily comparable with that found for *Phaeodactylum* in the present investigation.

A further estimate of the weight of organic matter produced in the *Phaeodactylum* cultures may be made from pH changes. Two examples have been selected:

	Date	Time	Temp. °C	Cell count/ mm³	pH
Ser. V, Jar 6	29 May	12:00	18	230	8.1
	4 June	08:30	15	908	8.5
Ser. IV, Jar 8	30 Apr.	08:00	11	310	7.6
	4 May	08:00	13	1,020	8.3

(From the results on p. 121 the average salinity has been assumed as 30.7‰, *i.e.*, chlorinity 17‰.) The titration alkalinity and then the carbonate alkalinity have been calculated, from which the total CO_2 per liter can be deduced (cf. Harvey 1955).

For Series V, Jar 6, the total CO_2 on 29 May at 12:00 hours was 81.7 mg CO_2/L and this had dropped, owing to photosynthesis, to 72.7 mg CO_2/L at 08:30 hours on 4 June. If all the carbon had been converted into organic matter, then: $\frac{12}{44} \times 9$ mg C per liter should have been produced. But in the same period the cell increase was 678 (230 to

908) cells/mm³. Thus:

$$278 \times 10^6 \text{ cells} = \frac{12}{44} \times 9 \text{ mg of C.}$$

Therefore:

$$1 \times 10^6 \text{ cells} = \frac{12}{44} \times \frac{9}{678}$$

$$= 0.0036 \text{ mg of C.}$$

A similar calculation for the second example gives:

$$1 \times 10^6 \text{ cells} = 0.0049 \text{ mg of C.}$$

The average is:

$$1 \times 10^6 \text{ cells} = 0.0042 \text{ mg of C.}$$

This value may now be compared with the independent calculation based on the dry weight of organic matter in a harvested culture. This gave: 1×10^6 cells = 0.0087 mg of organic matter. Ketchum and Redfield (1949) give an empirical formula for cultured *Nitzschia* (*Phaeodactylum*) $C_{18}H_{30}N_2O_8$, which would suggest that $\frac{\text{weight of C}}{\text{weight of organic matter}} = \frac{216}{402}$. On this basis: 1×10^6 cells had $0.0087 \times \frac{216}{402}$ mg of C. Therefore: 1×10^6 cells = 0.0046 mg of C. The agreement between the two calculations is surprisingly good.

Variation in the cell contents of phytoplankton species with culture conditions has been recognized for some time (cf. dry weights for *Chlorella*, Burlew 1953). Ketchum (1939b) demonstrated variations in cell content in *Nitzschia*. In the present work on *Phaeodactylum* it was also fairly clear from the differences in color between cultures of approximately the same cell density that the weight of dry matter varied with culture conditions. Nevertheless, on the basis of the few cultures that have been harvested, it is possible to calculate approximately the weight of organic matter which may be obtained from a large tank culture. The tanks (5 × 5 ft.) have now been shallowed. With ca. 10 to 12 in. depth of culture, compensation depth experiments suggest that the whole layer should be productive provided some extra illumination is given over winter. Each tank will hold then about 600 liters of culture, and if it is possible to grow a density of about 30,000 *Phaeodactylum*/mm³ on the tank scale, total harvesting of a single crop from one tank should yield about 194 g dry weight $\left(\frac{600 \times 10^6 \times 30{,}000 \times 0.0108 \times 10^{-3}}{10^6} = 194.4 \text{ g}\right)$. Of this ca. 157 g would be organic matter. Thus the production of organic matter expected from a tank 1 m² would be just under 70 g.

Harvey (1950) has estimated about 120 to 200 g of organic matter below a square meter for the English Channel, as the total production for a year. Using Riley's figure, he also estimates about 270 g as the total yearly production for the richer Gulf of Maine area. These calculations are based on such values as P and N decrease, pH change, etc. The present estimate, based on weight of dry organic matter obtained in culture, suggests that about one-third the annual production of a natural area should be achieved in a single crop grown in approximately 3 to 4 weeks. A continuous intensive production of *Phaeodactylum* with repeated harvesting of part of the crop would, however, be followed in any large-scale development.

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Particulate Iron in Offshore Waters of the Panama Bight and in the Gulf of Panama

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ABSTRACT

Particulate iron is reported from replicate samples taken at two depths at several locations in the Panama Bight during November 1955, and in replicate samples taken at two depths at a single inshore location in the Gulf of Panama at bimonthly intervals from December 1954 through December 1955. In addition, a few samples were taken at other locations in the Gulf of Panama and from a river flowing into the Gulf. The content of particulate iron, both in the Panama Bight and in the Gulf, shows highly contagious distributions, necessitating a logarithmic transformation to make the data amenable to statistical analysis. All samples from the Panama Bight could have arisen from a single log-normal distribution with a mean of 12.2 μg/L. In the Gulf of Panama, there is significantly higher iron in the surface (115.2 μg/L) than at 30 meters (62.1 μg/L) during the early part of the year when the standing crops of plankton organisms are high. Particulate iron content is higher inshore in the Gulf of Panama than offshore in the Panama Bight, and two samples from the Río Escota, containing 692 and 863 μg/L, were much higher than in the Gulf, indicating that possibly the iron is being brought in by runoff. From comparison of iron content in inshore and offshore waters, in both of which biological production is high, it is inferred that particulate iron cannot be a limiting factor on phytoplankton growth in the inshore waters.

INTRODUCTION

Particulate iron in marine waters is of considerable interest because it is the form in which iron is utilized by phytoplankton organisms (Goldberg 1952, Harvey 1937). It may, in some circumstances, be a limiting constituent for the growth of these microscopic plants.

Lewis and Goldberg (1954) investigated the iron content of waters at different depths from a number of stations in the North Pacific. They concluded that particulate iron tends to be more abundant in the upper layers (less than 500 meters) than in deeper layers, at least at some stations in the Northeast Pacific, and that the variability of results from replicate samples from the upper layer is quite high. It was inferred that "the marine biosphere acts as a reservoir for iron particles and accentuates the high scatter of the particulate iron and distribution."

In order to investigate the content of particulate iron in near-surface waters in an offshore and an inshore situation in the Tropical Eastern Pacific, and in order to investigate in somewhat more detail the nature of the distribution of particulate iron, two series of data have been collected: (1) replicate samples at two depths (ca. 10 meters and 65 meters) at nine stations in the Panama Bight, offshore from Panama and Colombia, occupied during November 1955 on the "Eastropic" expedition of the Scripps Institution of Oceanography; (2) replicate samples at two depths (10 meters and 30 meters, near the bottom) at a fixed inshore station in the Gulf of Panama occupied at biweekly intervals from December 1954 to December 1955. The latter series of data was part of a time-series observation of a number of physical and biological properties at this station made by personnel of the Inter-American Tropical Tuna Commission in connection with a study of the ecology of the Gulf of Panama. Replicate samples were also taken on one occasion at two other locations in the Gulf of Panama, and from a river flowing into the Gulf.

In every case, the analysis for particulate iron was made on a sample of approximately one liter of seawater, following the procedures of Lewis and Goldberg (1954). The

analyses were made by Mr. Minoru Koide, Research Chemist of the Scripps Institution of Oceanography, whose assistance in this study is gratefully acknowledged. The basic data are presented in Tables 1, 3, and 5, the concentrations of particulate iron being expressed as micrograms per liter of water.

TABLE 1. *Particulate iron content of replicate samples at nine stations in the Panama Bight*

Station No.	Position Lat. N	Position Long. W	Date		Particulate iron micrograms per liter "Shallow"	Particulate iron micrograms per liter "Deep"
ET-H-46	5° 00′	78° 09′	14 Nov. 1955		9.7	1.5
					12.6	13.0
					72.8	9.6
				mean	31.7	8.0
ET-H-47	5° 49′	78° 31′	15 Nov. 1955		18.2	11.1
					9.1	22.9
					16.1	12.9
				mean	14.5	15.6
ET-H-48	6° 52′	78° 54′	15 Nov. 1955		4.6	2.2
					8.4	8.4
					5.6	7.1
				mean	6.2	5.9
ET-H-49	7° 42′	79° 20′	16 Nov. 1955		8.8	14.7
					30.2	6.3
					5.1	6.2
				mean	14.7	9.1
ET-H-49A	8° 20′	79° 21′	16 Nov. 1955		6.4	6.7
					2.6	4.1
					9.3	10.7
				mean	6.1	7.2
ET-H-52	5° 43′	80° 31′	19 Nov. 1955		22.0	4.4
					82.0	11.9
					10.9	12.4
				mean	38.3	9.6
ET-H-53	4° 37′	81° 02′	20 Nov. 1955		9.1	4.2
					0	4.0
					6.6	6.2
				mean	5.2	4.8
ET-H-54	4° 08′	81° 48′	20 Nov. 1955		12.4	3.6
					9.1	9.1
					41.1	2.4
				mean	10.9	5.0
ET-H-55	3° 01′	82° 15′	21 Nov. 1955		6.6	2.8
					2.0	2.8
					7.2	3.0
				mean	5.3	2.9
			Arithmetic means of all observations		15.9	7.7
			Means of all observations, derived from transformed data		19.5	7.4
						12.2

OBSERVATIONS AT STATIONS IN THE PANAMA BIGHT

The positions of the nine stations, which were located in the Panama Bight, are given in Table 1 and are shown by solid circles in Figure 1. At each of these stations three one-liter samples were taken from each of the two depths. The "shallow" samples were taken in the mixed layer, with a wire length of 10 meters, except for ET-H-48 where only 5 meters were used. The "deep" samples were all taken with 65 meters of wire out, which, at every station, corresponded to a point within the thermocline, below the mixed layer (Anon. 1956). The content of particulate iron is shown in Table 1 for each sample, together with the means for each depth at each station, and the grand mean of all observations for each of the two depths. The average content of particulate iron at these stations appears to be very similar to that found by Goldberg and Lewis in the upper layer of the sea near the coast of California (their Figure 1) and and at their stations 7, 12, and 20 in the Northeast Pacific.

FIG. 1. Gulf of Panama and Panama Bight, showing locations at which samples were taken for particulate iron.

TABLE 2. *Analyses of variance of samples from the Panama Bight*

Source of variation	Degrees of freedom	Sum of squares	Mean square	Variance ratio
Raw data				
Total	53	11,751		
Depths	1	932	932	4.86*
Stations	8	2,338	292	1.53
Interaction	8	1,583	198	1.03
Samples at same position	36	6,897	192	
Transformed data				
Total	53	10.7011		
Depths	1	0.5451	0.5451	3.12
Stations	8	2.5938	0.3242	1.86
Interaction	8	1.2796	0.1599	0.92
Samples at same position	36	6.2832	0.1745	

* Significant at 5% level

An analysis of variance[1] of the raw data (Table 2) indicated that there was possibly a difference in the mean iron content at the two depths, but that there was no reason to suspect any differences between stations, and there was apparently no significant station-depth interaction. Comparing the variances among all samples for each of the two depths, a ratio of 15.85 was obtained, which is highly significant and indicates that possibly there was a difference in the variance about the mean values of the two depths. This analysis assumes, of course, normality in the distribution which was in fact not true. Since, however, deviations from normality tend to err in the direction of giving significant results when they do not really exist (Barnes 1952, p. 63), rather than the contrary, the conclusions from the analysis of variance of the raw data that there was no significant difference between stations was deemed sufficient basis for amalgamating all observations at each depth to examine the nature of the distributions. The variances among all samples at each depth (judged by a Chi-square test) were clearly larger than the mean, so that the iron content was not distributed according to a single Poisson distribution. It was apparent that the iron content follows some type of "contagious" distribution.[2]

To describe observations of this kind there have been proposed several types of distribution functions, which may be employed to transform the data so that they will satisfy the conditions for analysis of variance. A suitable transformation may be selected from examination of the relationships between the means and variances of the observations. For discussion of the various types of transformations that may be employed to normalize "contagious" distributions, and the criteria upon which they may be selected, the reader is referred to Barnes (1952) and Anscombe (1950). We have, therefore, computed the means and variances for each of the sets of three replicate observations given in Table 1. In Figures 2 and 3 are plotted the means and standard deviations (square root of the variance) for the nine sets of observations at the "shallow" and "deep" sampling levels, respectively. It may be seen that, in each case, the standard deviation is roughly proportional to the mean, although the proportionality constant appears to be smaller for the deep than for the shallow observations. This suggests that a logarithmic transformation will stabilize the variance in each case (Barnes 1952). Since there is one zero value, it is necessary to add a constant to all the values before taking the logarithms. We have, therefore, employed the transformation

$$X' = \log_{10} (10X + 1)$$

where X is the particulate iron in μg/liter and X' is the transformed variate.

The effect of this transformation in stabilizing the variances is shown in Figure 4, where the standard deviations of X' are plotted against the mean values of X' for each set of three replicates. It may be seen that these means and standard devia-

[1] Analysis of variance in this paper follows the methods of Snedecor, 1946, Chapter 11.

[2] A distribution is "contagious" when the occurrences of the variate measured are not random in space, but are "clumped" so that the probability of occurrence is not uniform throughout the space.

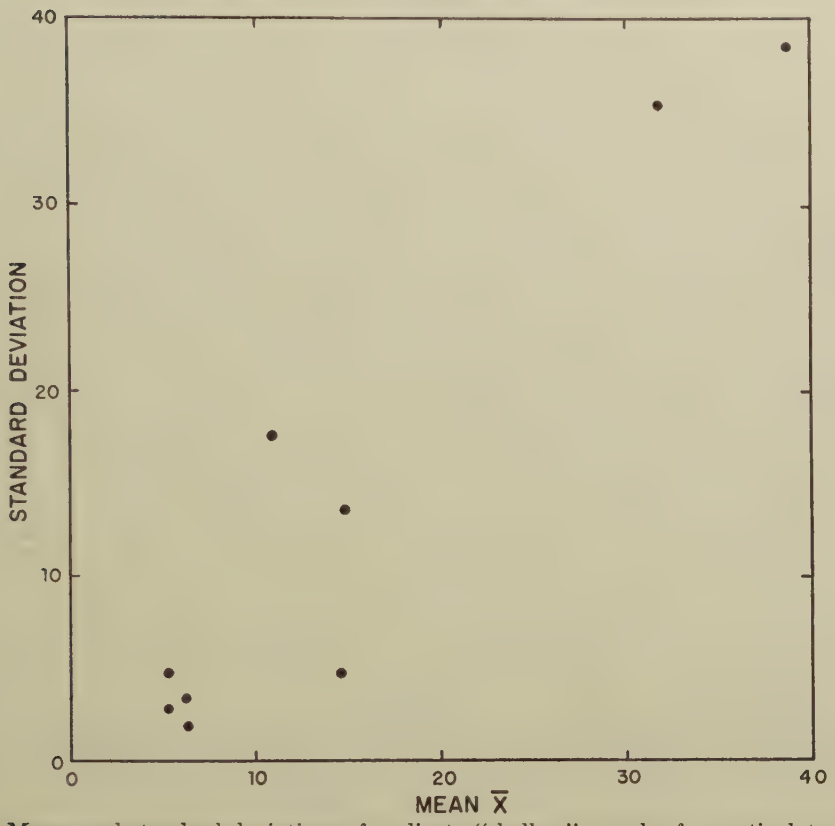


FIG. 2. Means and standard deviations of replicate "shallow" samples for particulate iron in the Panama Bight.

tions are not correlated. Furthermore, comparison of the variances about the means of all samples at each depth indicated no significant difference.

The analysis of variance of the transformed data (Table 2) indicates that there are no significant differences between stations or between depths, and no significant interaction.

It may, therefore, be concluded that the observed values at all stations at both depths in the Panama Bight could have been drawn from a single "population" of iron particles with a contagious distribution. The best estimate of the mean value, obtained from the transformed data, is 12.2 μg/L. This is computed by taking the mean of the transformed values, adding 1.15 times the variance and transforming back (Barnes 1952). This value and similar estimates of the means for the "shallow" and "deep" series are also shown in Table 1.

OBSERVATIONS IN THE GULF OF PANAMA

Serial data from a fixed location in the Gulf

One-liter water samples were taken in replicate, by repeated casts, from two different depths, at bimonthly intervals between December 24, 1954, and December 12, 1955, at a single location in the Gulf of Panama (79°23′ W, 8°45′ N) about 10 miles southeast of Taboga Island, shown by a star in Figure 1. At this location the depth of the Gulf is about 40 meters, varying with the stage of the tide, which has a spring range in the Gulf of Panama of about 5 meters. With a few exceptions three samples were taken from the surface and three from 30 meters. The exceptions were the omissions of one surface sample on April 5 and one deep sample each on May 3 and August 22. The deep samples on April 19 were taken at 40 meters instead of 30 meters, but this has been disregarded in subsequent

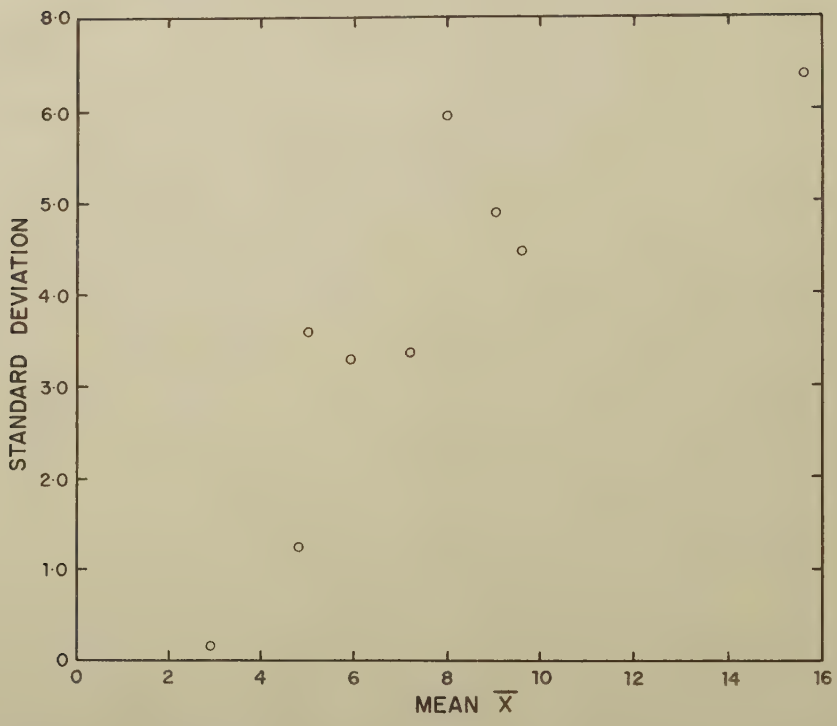


FIG. 3. Means and standard deviations of replicate "deep" samples for particulate iron in the Panama Bight.

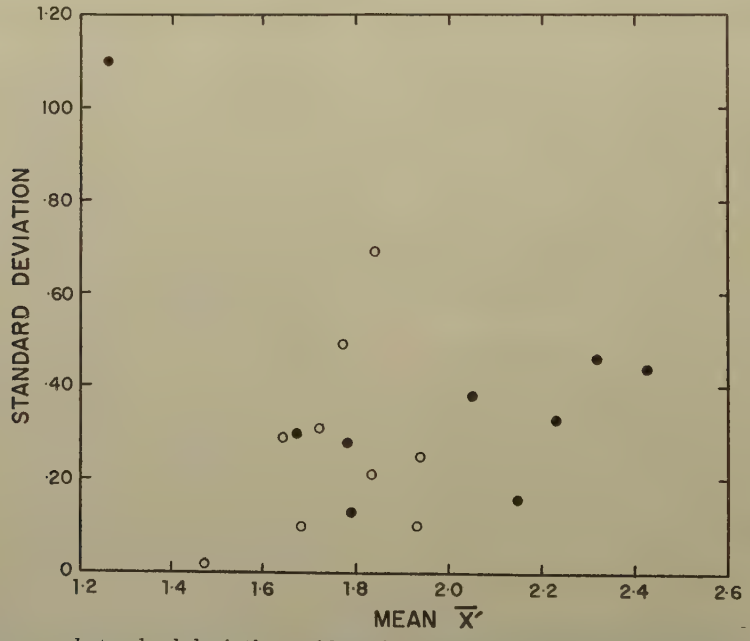


FIG. 4. Means and standard deviations of logarithmic transformation of values of particulate iron in sets of replicate samples in the Panama Bight. Solid circles represent "shallow" samples; open circles represent "deep" samples.

analyses, since the values of the iron content were well within the range of those obtained at 30 meters on other dates. The basic data, together with the mean values for each depth at each station and the grand means of all observations at each depth, are given in Table 3. Salinity values at the surface and 30 meters are also tabulated; salinities were determined by the standard method of titration with silver nitrate.

It may be noted that the average particulate iron content of these inshore waters is several times higher than that of offshore waters in the Panama Bight. It also appears that the particulate iron is, on the average, more abundant in the surface samples than at 30 meters. Here again, however, there is rather considerable variation among replicates and among the means of the samples taken on different dates.

The large variability among replicates suggests that we are again dealing with some contagious distribution. Therefore, we have plotted in Figures 5 and 6 for the surface and 30-meter samples, respectively, the means and standard deviations of each set of replicate samples. It may be seen from these figures that the variances are too large relative to the means to apply the Poisson distribution, and that the standard

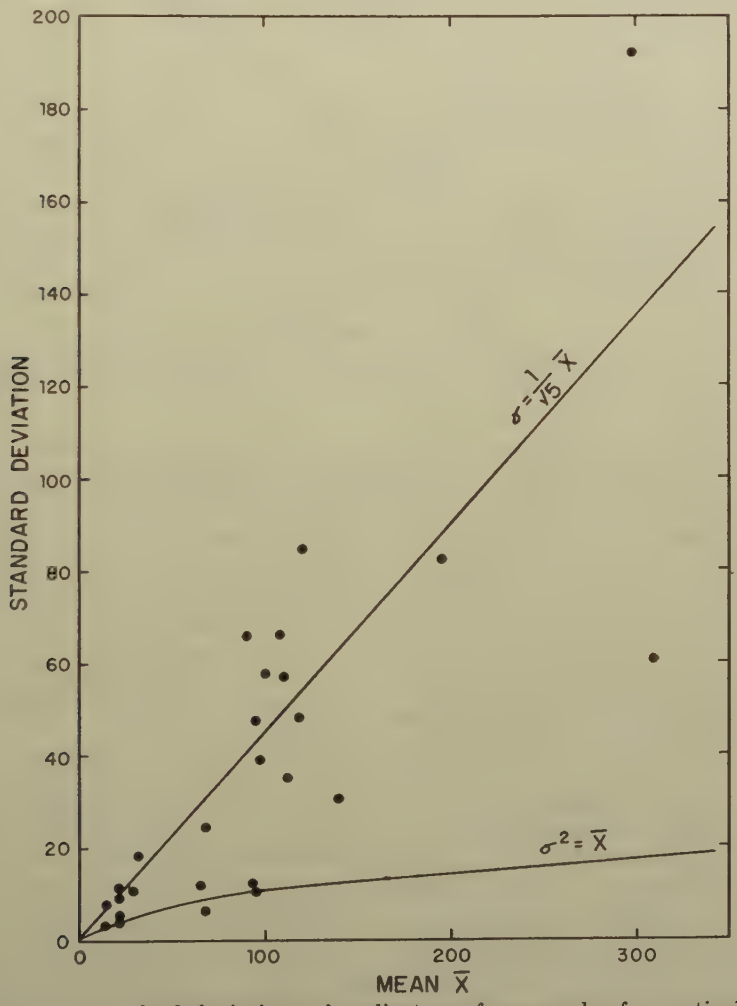


FIG. 5. Means and standard deviations of replicate surface samples for particulate iron at the fixed location in the Gulf of Panama.

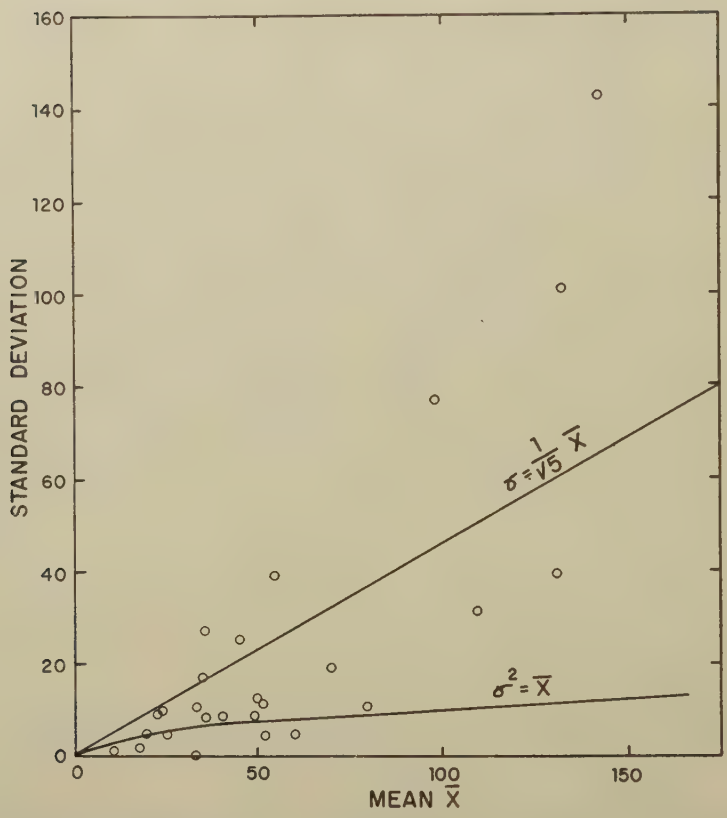


FIG. 6. Means and standard deviations of replicate 30-meter samples for particulate iron at the fixed location in the Gulf of Panama.

deviations appear to be roughly proportional to the means, the proportionality constant being, in each case, close to $1/\sqrt{5}$. A logarithmic transformation should, therefore, stabilize the variance and permit the use of analysis of variance to compare depth and time differences. We have, therefore, employed the transformation $X' = \log_{10} X$.

In Figure 7 are shown graphically the means of the logarithms of the measurements of particulate iron, at each depth at each station, and also the salinities at corresponding stations and depths.

In Figure 8 are plotted, for each set of replicate samples, the mean of X' against the standard deviation. It may be seen that, while the standard deviations show much scatter, they are no longer correlated with the means. We have employed this transformed variate in analysis of variance to examine differences among stations and depths (Table 4).

It may be seen that, considering all observations, there were much greater differences between the average values at each of the two depths, and among the average values from station to station, than could be expected from the variability observed among replicate samples. That the difference between depths is not consistent at different stations (dates) is shown by the significantly high depth-station interaction.

It may be noted, however, from Figure 7 that up to July or August the iron content seems to be consistently higher at the surface than at 30 meters. It has been shown by Schaefer (1957, Fig. 10) that the plankton organisms are more abundant at this location in the Gulf of Panama during the first half of the year than subsequently, presumably due to the effects of upwelling from January to April. It may be, therefore, that the particulate iron content is

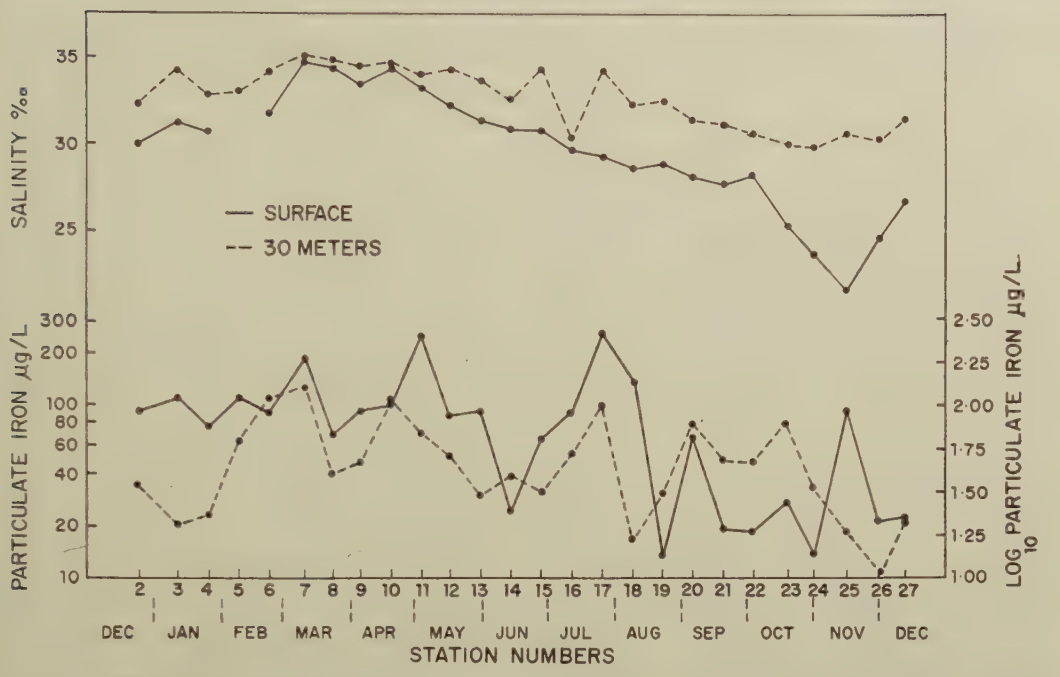


FIG. 7. Mean values of logarithm of particulate iron and values of salinity at the surface and 30 meters at the fixed location in the Gulf of Panama.

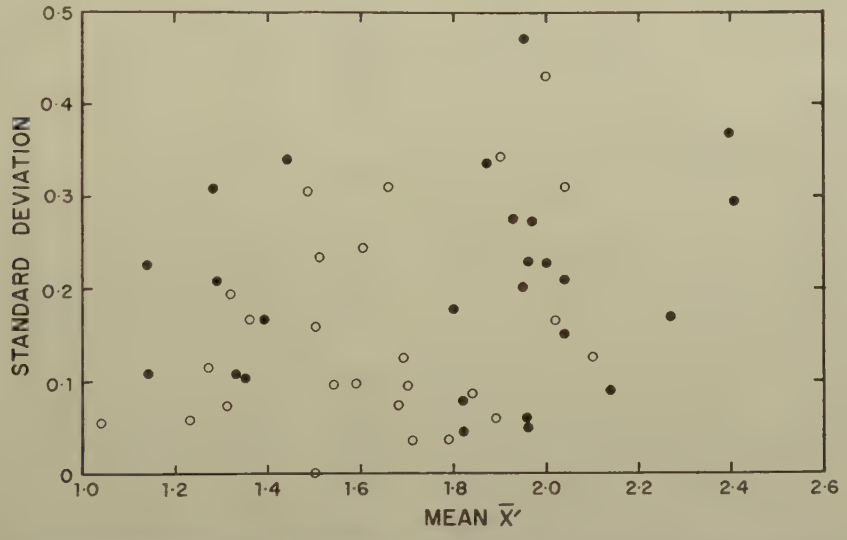


FIG. 8. Means and standard deviations of logarithmic transformation of values of particulate iron in sets of replicate samples taken at the fixed location in the Gulf of Panama. Solid circles represent surface samples; open circles represent 30-meter samples.

maintained at a higher level near the surface during the early part of the year by biological action, but that later in the year this effect is no longer evident. In order to examine this, we have made separate analyses of the particulate iron data for Stations 2–16 (24 December 1954 through 11 July 1955) and for Stations 17–27 (25 July 1955 through 12 December 1955).

During the early part of the year the mean

TABLE 3. *Particulate iron content of replicate samples at a fixed location in the Gulf of Panama (79° 23′ W 8° 45′ N.) occupied at bimonthly intervals from December 1954 to December 1955*

Station number	Date	Particulate iron, micrograms per liter								Salinity ‰[2]	
		Surface			Means (arithmetic)	Deep (30 meters)			Means (arithmetic)	Surface	30 meters
2	24 Dec. 1954	167.0	69.2	64.8	100.3	45.5	29.9	32.5	36.0	30.01	32.4
3	11 Jan. 1955	133.0	72.8	134.0	113.3	21.9	31.0	24.8	25.9	31.16	34.2
4	25 Jan. 1955	163.0	35.9	70.2	89.7	17.9	35.6	18.4	24.0	30.77	32.9
5	8 Feb. 1955	153.3	138.3	63.1	118.2	55.6	62.5	65.2	61.1	(lost)	33.0
6	22 Feb. 1955	105.0	129.0	53.2	95.7	82.3	249.0	65.2	132.2	31.76	34.2
7	10 Mar. 1955	166.0	135.0	290.0	197.0	175.0	117.0	100.0	130.7	34.67	35.0
8	23 Mar. 1955	77.4	68.8	53.1	66.4	23.9	73.3	37.5	44.9	34.41	34.8
9	5 Apr. 1955	101.0	83.6	—	92.3	39.9	24.0	98.4	54.1	33.21	34.5
10	19 Apr. 1955	60.6	95.8	172.0	109.5	113.0[1]	145.0[1]	67.8[1]	108.6	34.20	34.6
11	3 May 1955	359.0	468.0	96.4	307.8	84.0	56.7	—	70.4	33.16	34.0
12	16 May 1955	122.0	125.0	41.0	96.0	47.7	63.8	41.9	51.1	32.10	34.3
13	30 May 1955	180.0	89.5	51.0	106.8	67.7	19.8	20.3	35.9	31.42	33.6
14	13 Jun. 1955	21.1	38.0	18.3	25.8	41.6	47.5	30.6	39.9	30.99	32.6
15	27 Jun. 1955	70.2	89.1	40.3	66.5	21.5	42.9	33.4	32.6	30.86	34.4
16	11 Jul. 1955	189.0	144.0	25.6	119.5	47.4	55.9	52.0	51.8	29.59	30.4
17	25 Jul. 1955	255.0	128.0	507.0	296.7	306.0	76.3	44.2	142.2	29.29	34.2
18	8 Aug. 1955	132.0	173.0	113.0	139.3	16.4	19.5	15.0	17.0	28.65	32.3
19	22 Aug. 1955	11.1	18.5	13.1	14.2	31.6	31.4	—	31.5	28.98	32.5
20	5 Sept 1955	69.6	68.9	58.2	65.6	83.2	86.5	66.9	78.9	28.16	31.5
21	19 Sept 1955	12.0	31.6	19.1	20.9	41.4	64.2	44.2	49.9	27.84	31.1
22	3 Oct. 1955	8.1	24.8	31.0	21.3	42.6	58.0	44.8	48.5	28.33	30.6
23	19 Oct. 1955	44.9	11.5	40.5	32.3	37.9	184.7	71.2	97.9	25.20	30.0
24	31 Oct. 1955	13.8	8.1	23.1	15.0	51.9	17.8	36.0	35.2	23.61	29.9
25	15 Nov. 1955	104.4	90.0	83.3	90.6	13.9	24.0	18.7	18.9	21.68	30.6
26	1 Dec. 1955	27.7	21.5	16.8	22.0	10.5	9.9	12.5	11.0	24.61	30.4
27	12 Dec. 1955	17.1	24.1	27.3	22.8	12.6	30.2	23.7	22.2	26.82	31.5
Arithmetic means					94.2				56.0	29.66	32.67
Means derived from transformed data					86.4				55.9		

[1] Taken at 40 meters

[2] Surface salinities are observed values. 30 meter salinities are interpolated values.

logarithms of particulate iron content were 1.9569 at the surface and 1.6863 at 30 meters. Corresponding means of 115.2 and 62.1 μg/L respectively are obtained when each mean logarithm is added to 1.15 times its variance and transformed back to the original units. It is shown clearly by Table 4 that this difference is highly significant. The analysis of variance for these stations shows also that there was, during this period, more variation among the values obtained on different dates than could be expected from the variation among replicates, but the fact that the depth-station interaction is non-significant demonstrates that the depth difference is consistent from station to station.

During the latter part of the year the mean logarithms of particulate iron content were 1.5708 at the surface and 1.5491 at 30 meters. Corresponding means of 64.2 and 46.6 μg/L respectively are obtained when each mean logarithm is added to 1.15 times its variance and transformed back to the original units. It is evident from the analysis of variance that this small difference is no greater than could be expected from the variability among replicates. During this period, however, there is a significantly high variation among station means and significant station-depth interaction. This indicates that the differences between values obtained at the two depths on different dates were significantly high with respect to the variations among replicates, but that the depth differences were not consistent from station to station.

It may be seen from Figure 7 that the

salinity at this location in the Gulf of Panama declined progressively during the period May-November, the decline being more rapid at the surface than in the deeper layers. This corresponds to the period of heavy rainfall, which reaches a maximum in October. It seemed possible that the precipitation differentially diluting the surface layer might sufficiently decrease the particulate iron per unit volume to mask any effect of biological activity in maintaining a concentration near the surface. We have, therefore, also calculated the iron/salinity ratio for each of our samples. The station means of the logarithms of this ratio for each depth are shown graphically in Figure 9. It may be seen that this graph exhibits the same general features as Figure 7, indicating a higher iron/salinity ratio at the surface than at 30 meters during the early part of the series, but no apparent difference in the latter part of the year. To examine this critically, we have made an analysis of variance of these data, again treating separately the observations for Stations 2–16 and 17–27. Results were the same as before, *i.e.*, a highly significant difference between depths for the first period and no significant difference between depths for the last part of the series. The differential concentration of particulate iron in the surface water is, therefore, demonstrable only during the early part of the year, and is very likely due to the biological activity of the large numbers of plankton organisms present during that time.

TABLE 4. *Analyses of variance of logarithms of particulate iron in samples taken at the fixed location in the Gulf of Panama*

Source of variation	Degrees of freedom	Sum of squares	Mean square	Variance ratios
All observations:				
Total	152	21.7028		
Depths	1	1.0153	1.0153	1.0153/0.0454 = 22.36†
				1.0153/0.2083 = 4.87*
Stations (dates)	25	10.8919	0.4357	0.4357/0.0454 = 9.60†
Interaction	25	5.2076	0.2083	0.2083/0.0454 = 4.59†
Replicates (samples at same position)	101	4.5880	0.0454	
Early (Stations 2–16)				
Total	87	8.7068		
Depths	1	1.6112	1.6112	1.6112/0.0487 = 33.08†
Stations (dates)	14	3.1970	0.2284	0.2284/0.0487 = 4.69†
Interaction	14	1.0739	0.0767	0.0767/0.0487 = 1.57
Replicates (samples at same position)	58	2.8247	0.0487	
Late (Stations 17–27)				
Total	64	10.4394		
Depths	1	0.0077	0.0077	0.0077/0.0410 = 0.19
Stations (dates)	10	5.1385	0.5139	0.5139/0.0410 = 12.53†
Interaction	10	3.5300	0.3530	0.3530/0.0410 = 8.61†
Replicates (samples at same position)	43	1.7632	0.0410	

* Significant at 5% level.
† Significant at 1% level.

Other data from the Gulf of Panama

On 29 and 30 November 1955 replicate samples of approximately one liter each were taken at a depth of 10 meters at two other locations in the Gulf of Panama and analyzed for particulate iron. The data are reported in Table 5 and the positions of the stations shown in Figure 1 by open circles.

Puerto Mensabe is located on the western shore of the Gulf, about 20 miles inside Cape Mala. Results from the samples from this inshore location are quite similar to the values obtained during the latter part of the year at the location near Taboga Island (Table 3), which is also fairly well inshore; the mean logarithm for the Puerto Mensabe station is 1.4262, whereas for the fixed station in the Gulf of Panama during the latter part of the year the mean logarithms were 1.5708 at the surface and 1.5491 at 30 meters.

The location off San José Island is, on the contrary, well out in the Gulf, being not far from Station ET-H-49 of the Panama Bight sampling series. At this offshore location the particulate iron values are similar to those obtained at 10 meters at other locations in the Panama Bight (Table 1). However, the difference between the mean logarithm of the values at this single location (1.1517) and the mean logarithm of surface samples at the fixed location near Taboga Island in the latter part of the year (1.5708) cannot be judged as necessarily significant in the light of the sampling variance of 0.5139 (Table 4) among values obtained at the same location on different dates.

These results suggest that there may be

an offshore gradient of particulate iron in the Gulf of Panama, and this together with the obvious difference between the values obtained inshore in the Gulf and offshore in the Panama Bight, further suggests that the iron is coming in from the land.

This appears to be confirmed by samples taken from the Río Escota, a tributary of the Río Santa María, which flows into the west side of the Gulf of Panama (Bahía Parita). The position is shown by an open circle in Figure 1. These samples were from estuarine waters, since the lower reaches of these rivers are actually estuaries. Two samples of one liter each were taken on 20 November 1955. Because of the turbidity it was not possible to pass the entire samples through a millipore filter. Consequently, the particulate iron was measured in aliquots of 370 ml for one sample and 300 ml for the other, giving 692 and 863 μg/L respectively (Table 5). It may be seen that the particulate iron content of these samples is a great deal higher than that of samples taken in the Gulf.

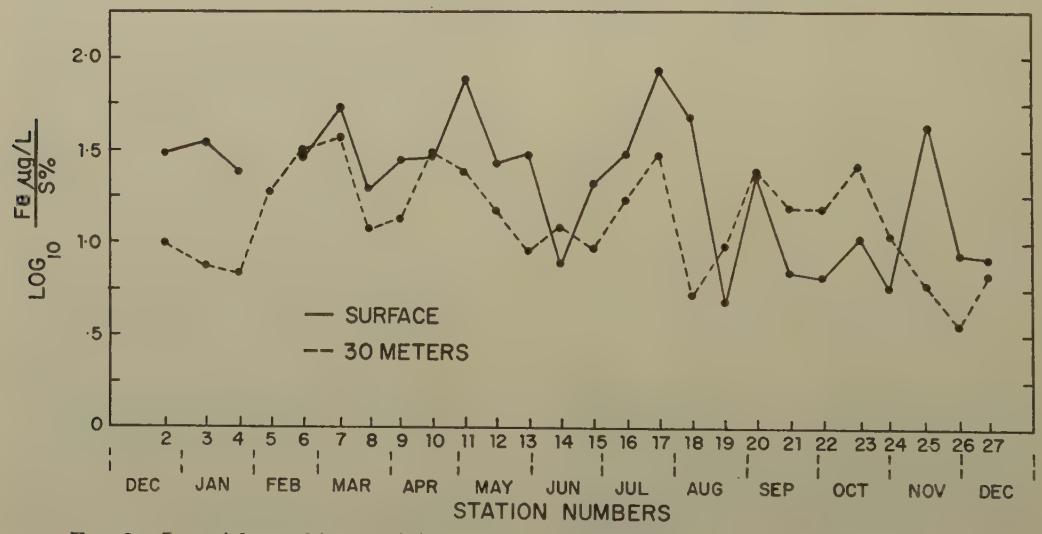
TABLE 5. *Other particulate iron samples from the Gulf of Panama*

Position	Date	Depth	Particulate iron micrograms per liter	$\log_{10}$
28 miles SSE of Southern end of San José Island	29 Nov., 1955	10 meters	18.6	1.2695
			13.1	1.1173
			11.7	1.0682
			mean 14.5	1.1517
5 miles E of Puerto Mensabe	30 Nov., 1955	10 meters	26.3	1.4200
			25.7	1.4099
			28.1	1.4487
			mean 26.7	1.4262
Rio Escota (8° 04′ 30″ N, 80° 29′ 30″ W)	20 Nov., 1955	Surface	692	
			863	
			mean 778	

DISCUSSION

It has been shown that both in the offshore waters of the Panama Bight and in the inshore waters of the Gulf of Panama the content of particulate iron exhibits "contagious" distributions. For the statistical analysis of samples from such distributions by the analysis of variance, it is necessary to employ a transformation to approximately normalize the distributions. A logarithmic transformation appears to be adequate for this purpose in the case of our data on particulate iron. Re-examination of the data of Lewis and Goldberg (1954) from their Stations 7, 12, 20, and 47 in the Northeast Pacific also indicates that the sampling distributions of particulate iron at these locations were of a similar type.

It may be that the contagious type of distributions of particulate iron is due in


LOG10 Fe µg/L / S‰
2·0
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— SURFACE
-- 30 METERS
2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27
DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
STATION NUMBERS

FIG. 9. Logarithms of iron-salinity ratio at the fixed location in the Gulf of Panama.

large part to the activity of the marine biosphere, as concluded by Lewis and Goldberg. This, however, is not *necessarily* true. Such distributions *could* arise from the occurrence of particles of iron of a variety of sizes, each size being distributed in the water completely at random (Anscombe 1950). It would be desirable to examine the distributions of particle sizes in order to investigate this matter further.

On the other hand, the occurrence of significantly higher average particulate iron content, at least on some occasions, associated with the marine biosphere, indicates that the organisms do modify the distribution of iron due to purely physical processes. Lewis and Goldberg's data show that the iron content of the upper 500 meters at some stations in the Northeastern Pacific is significantly greater than in deeper layers. (This result is obtained even when their data are re-analyzed employing a logarithmic transformation to normalize the sampling distribution.) The observations from off Taboga Island in the Gulf of Panama indicate clearly that the particulate iron content at the surface is higher than at 30 meters during the period of high standing crops of plankton organisms.

There is rather good evidence that the iron in the region of the Gulf of Panama and Panama Bight is being brought into the sea by runoff from the land. Particulate iron in the lower reaches of one of the rivers flowing into the Gulf was found to be much higher than the iron content at an inshore location in the Gulf, and the latter in turn is significantly greater than the iron content at offshore stations in the Panama Bight. A single group of 3 replicates from the outer part of the Gulf of Panama off San José Island showed a mean iron content comparable to the values encountered elsewhere in the Panama Bight; however, since this value was within the range of sampling variation at the inshore station near Taboga Island, this particular evidence of an offshore gradient of particulate iron in the Gulf is not conclusive.

Since the particulate iron content of inshore waters in the Gulf is higher than at locations offshore in the Panama Bight, and since the latter are biologically very productive (Holmes, Schaefer, and Shimada 1957), it seems unlikely that iron can be a limiting factor on phytoplankton growth in these inshore waters.

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The Limnology of Canyon Ferry Reservoir

I. Phytoplankton-Zooplankton Relationships in the Euphotic Zone during September and October, 1956

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ABSTRACT

Phytoplankton and zooplankton standing crop, gross and net primary production were measured. From these data the daily rate of loss of phytoplankton from the euphotic zone was calculated. The phytoplankton loss correlated well with zooplankton during September and with vertical water movement during October. A grazing coefficient was calculated (G = 1.064 L water/mg dry wt. zooplankton/day). By use of this coefficient the loss of phytoplankton by zooplankton grazing was calculated for the period of study and averaged 0.255 mg glucose/L/day. Zooplankton assimilation averaged 0.216 mg glucose/L/day, indicating a digestive efficiency of 85%. Gross and net primary production from September 6 to October 17 amounted to 137.2 and 114.0 g glucose/m^2, respectively. Zooplankton assimilation was estimated to be 85% of net primary production. The ratio of zooplankton net production to zooplankton assimilation was 10.5%.

INTRODUCTION

Canyon Ferry Reservoir is an artificial impoundment located on the Missouri River near Helena, Montana. The dam was built by the United States Bureau of Reclamation, and the reservoir was filled for the first time during 1955. The reservoir extends upstream from the dam about 25 miles to a point near Townsend, Montana. At maximum operating pool level (3,800 feet m.s.l.), the reservoir has a capacity of 2,050,900 acre-feet, a surface area of 35,180 acres, and a maximum depth of 165 feet.

The purpose of the present study is to determine primary and secondary productivity over a period of years. Financial support for this investigation was provided by the National Science Foundation.

METHODS

Samples taken with a three-liter Kemmerer water bottle at the deep end of the lake near the dam, from the surface to 25 feet at five-foot intervals, were mixed in a large plastic container, and a series of 250-ml glass-stoppered bottles was carefully filled with water from the composite sample. A bottle was suspended from a float at each five-foot interval from the surface to 25 feet. In addition, two black bottles of water were suspended in the lake, and two bottles were immediately processed for oxygen determination. The bottles were set out at 9:00–10:00 A. M. and taken up six hours later. From changes in oxygen concentration in the clear and black bottles, gross photosynthesis and respiration were computed.

A 100-ml sample was collected from the composite mixture, preserved with six drops of Lugol's solution and allowed to stand until the plankton had settled out. As much as possible of the supernatant was poured off; the remaining fraction was centrifuged and the centrifugate made up to ten ml. A one-ml aliquot was placed in a Sedgewick-Rafter cell, and ten or twenty fields were counted under 100× magnification. Dimensions of the cells were estimated with a Whipple micrometer disk, and the volumes were computed using appropriate formulae.

In addition four liters of the composite sample were collected in a polyethylene bottle and immediately placed on ice. Upon return to the laboratory, one liter aliquots were centrifuged in a Foerst continuous flow centrifuge for chlorophyll and seston determinations.

The residue collected for chlorophyll was

centrifuged in a clinical centrifuge, the remaining water was then poured off, and five ml of 90% acetone were added. The sample was placed in a deep freeze overnight, after which the acetone extract was separated from the residue by centrifugation. Chlorophyll concentration was determined with a Klett-Summerson colorimeter using a red filter. One Klett unit was assumed to be equal to 0.28 μg chlorophyll a/L.

The remainder of the composite sample (8–10 liters) was measured and poured through a #20 small Wisconsin net and preserved for determination of zooplankton.

All of the crustacean fraction of each net plankton sample was counted under a 40× binocular microscope, and the lengths and widths were measured with a Whipple micrometer disk. The average weight of individual animals was determined by picking out several animals and placing them on tared cover slips. The animals were oven-dried at 55°C overnight and weighed. From this information, the weight of zooplankton (Crustacea) per liter was estimated.

Rotifers were ignored, since their comparative number and volume would make their effect on the phytoplankton insignificant compared to the effect of the vastly greater weight of Crustacea.

On several occasions, composite samples were collected at five-foot intervals from the 30–55 and 60–90 foot zones, and at ten-foot intervals in the zone from 90 feet to the bottom. Cell volume, chlorophyll, and seston were treated as indicated above. Seston figures will not be given in this paper as they have not been found useful up to the present time.

STANDING CROP OF PHYTOPLANKTON AND ZOOPLANKTON IN THE EUPHOTIC ZONE

Cell volume (mm³/liter) and chlorophyll concentration (μg/liter) are given in Table 1. The phytoplankton was composed chiefly of blue-green algae (*Aphanizomenon flos-aquae* and *Polycystis aeruginosa*) and diatoms (*Stephanodiscus niagarae*, *Fragilaria crotonensis*, *Melosira granulata*, and *Asterionella formosa*). The mean percentages by volume were 53.2% blue-greens and 41.2% diatoms. Green algae were a relatively minor constituent. The values for cell volume following September 26 are not shown. After this date *Polycystis* replaced *Aphanizomenon* as the dominant alga. Because of the irregular shape of the colonies of *Polycystis* and fragmentation into individual cells, it was impossible to obtain accurate measurements of cell volume. For the dates where both cell volume and chlorophyll concentration are shown, there is fairly good correlation, since both show a peak early in September, a decline during the

TABLE 1. *Phytoplankton, zooplankton, photosynthesis, and respiration*

	September							October				Average
	6	8	11	17	22	26	30	3	7	14	17	
Phytoplankton												
cell volume—mm³/L	2.33	4.54	6.01	1.83	1.07	4.71						
chlorophyll—μg/L	1.93	5.06	3.92	2.32	1.51	4.20	2.80	3.08	2.24	2.24	3.08	2.94
Gross photosynthesis												
μmole O_2/L/hr	1.21	1.04	2.52	1.25	0.66	2.38	1.04	1.86	0.59	0.34	0.34	1.20
μmole O_2/mm³/hr	0.52	0.23	0.42	0.68	0.62	0.51						
μmole O_2/μg chlorophyll/hr	0.63	0.21	0.64	0.58	0.44	0.57	0.37	0.60	0.26	0.15	0.11	0.41
Black-bottle respiration												
μmole O_2/L/hr	0.00	0.78	1.56	0.69	0.26	1.00	0.51	0.26	0.00	0.00	1.30	0.58
Zooplankton												
number/L	6.00	18.30	44.80	54.90	26.90	28.80	12.38	6.82	4.25	4.51	6.80	19.50
mg dry wt/L	0.096	0.343	0.617	1.050	0.663	0.663	0.276	0.135	0.088	0.074	0.138	0.377

middle of the month and a rise late in September.

Number and weight of zooplankton per liter are shown in Table 1. Two species of *Daphnia* (*D. longispina* and *D. pulex*) were present. The species of *Cyclops* and *Diaptomus* are unknown. Nauplii and *Bosmina longirostris* population data are not included since they made up an insignificant fraction of the population.

Figure 1 shows the standing crop of phytoplankton and zooplankton on a weight basis. The chlorophyll concentration was used as a basis for estimating phytoplankton biomass by assuming that 5 μg chlorophyll are equivalent to 1.00 mg ash-free dry weight. Manning and Juday (1941) usually obtained values of 2–3 μg chlorophyll per mg seston and Riley (1941b) an average ratio of 4.2 μg chlorophyll per mg ash-free dry weight net plankton. However, both of these estimates of weight include some trypton as well as phytoplankton, although Riley's data, based on net plankton, would contain less. The value used in this study was derived by assuming that 1 mm^3 phytoplankton will have an ash-free dry weight of 0.20 mg, which is the factor that Hill and Whittingham (1953) cited for pure cultures of *Chlorella*. The average chlorophyll/cell-volume ratio from Table 1 was 1.03 μg chlorophyll/mm^3; hence 1 μg chlorophyll equals 1 mm^3 cells, equals 0.20 mg ash-free dry weight.

Zooplankton weight was estimated by multiplying the number of animals per liter by the average dry weight of animals determined in the method described previously.

Since the standing crop is a balance between the rate of production and the rate of loss, one must consider factors which affect these rates in attempting to explain variations in the standing crop.

Examination of Table 1 reveals that there was no decline in the rate of photosynthesis per unit of chlorophyll to account for the drop in phytoplankton during the middle of September. The average value of photosynthesis during September was 0.48 μmole O_2/μg chlorophyll/hr. Fluctuations from this value are probably due to differences in light and nutrients between the various sampling dates. The decline of the standing crop in October seems to be partially due to a decline in the rate of photosynthesis, since there is a distinct downward trend in the rates. The average of the October measurements was 0.28 μmole O_2/μg chlorophyll. Declining solar radiation is probably the explanation for the decline in photosynthesis in October (Ryther 1956, Verduin 1956).

The chief factors causing loss of phytoplankton from the euphotic zone would be turbulence and zooplankton grazing. Turbulence would have been less effective in causing loss during September than October, as there was a considerable thermal gradient

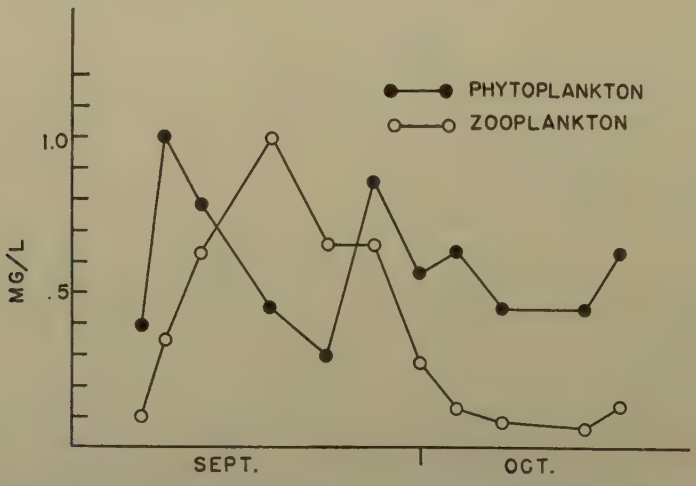

FIG. 1. Standing crop of phytoplankton and zooplankton in euphotic zone (surface to 25 ft).

in the epilimnion during September compared to October when the epilimnion was thermally homogeneous.

This inference is further supported from consideration of Figure 2 in which lines of equal phytoplankton and zooplankton density are plotted against depth and time. From September 6 to September 30, the populations of both zooplankton and phytoplankton were stratified; and after September 30, nearly complete vertical homogeneity is indicated.

The most important factor which could have caused loss of phytoplankton during September was grazing. The inverse relationship between phytoplankton and zooplankton gives strong presumptive evidence for this hypothesis. Presumably the rapid increase in phytoplankton during early September provided sufficient food for zooplankton to rapidly build up. As the zooplankton population continued to increase, the rate at which the phytoplankton was grazed became greater than the rate of production, and the standing crop declined. With decline of phytoplankton eventually the rate of grazing was not sufficient to maintain the assimilation of the existing zooplankton population which then declined in size. With decline of zooplankton and relaxation of grazing pressure, the rate of phytoplankton production exceeded the rate of loss, and the population built up again in late September. Declining photosynthesis and increased loss due to turbulence caused a gradual decline in early October until an approximate steady-state population of phytoplankton was attained in which photosynthesis balanced losses from turbulence and grazing.

The reciprocal relationship between zooplankton and phytoplankton shows up especially well in Figure 2. During the period of zooplankton increase at all depth levels there was a simultaneous decrease in phytoplankton at all depth levels, becoming practically zero (as measured by chlorophyll) below the 25-foot stratum on September 22 during the height of the zooplankton pulse. Following the decline of zooplankton, the population of phytoplankton increased at all levels.

In Figure 2*C* a line is drawn through the depth strata at which the *Daphnia* population averaged 1.3 mm in length. At depths above this line the average length was less than 1.3 mm, and at depths below, the average length was greater than 1.3 mm. The largest and oldest animals were at the deepest stratum (85 ft–bottom), and as the zooplankton population built up, the average size of the animals decreased.

Furthermore, the downward trend of the 1.3 mm isochore indicates that young individuals made up an increasingly greater proportion of the population at all depths, reaching a maximum ratio at the height of the zooplankton pulse (September 22–26). Following the zooplankton peak, older individuals made up an increasing proportion of the population at the deeper levels until October 3. Following this date, the same trend in variation of size occurred again and accompanied the increase of zooplankton that developed after October 14.

This relationship between size of animals and population growth corresponds with Slobodkin's (1954) observations on *Daphnia obtusa*: "In general, the peaks of population number correspond with the maximum proportion of small animals, the troughs with the maximum proportion of large animals." This relationship can be interpreted as follows. During the early stages of population growth, the relatively few large adults had a high reproductive rate, resulting in a size-frequency distribution that was skewed toward the small end. The population increase eventually gave rise to a population which was sufficient to reduce the food supply of all animals so that reproduction almost ceased. At this point the population was at its peak and consisted largely of small animals. As a result of the increased severity of competition for food, the death rate exceeded the birth rate and the population size declined. This reduced the grazing pressure on the phytoplankton and the surviving animals were able to obtain sufficient food, resulting in the shift of the size-frequency distribution toward a larger mean size. Concurrently, reproduction commenced again and the same cycle re-

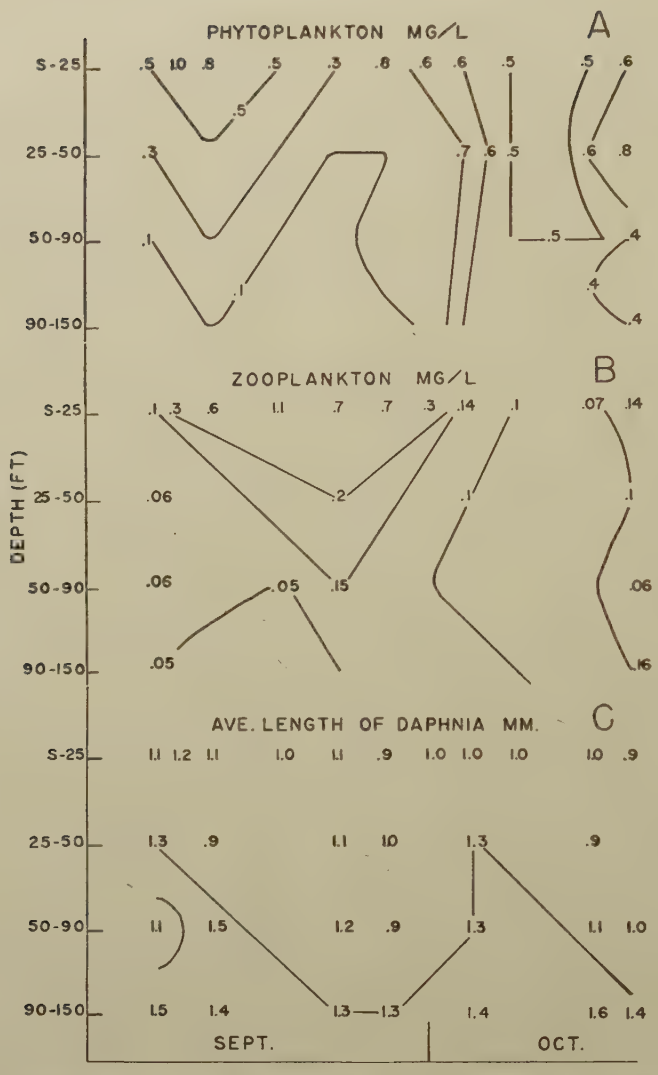

FIG. 2. Depth and time distribution of phytoplankton, zooplankton, and *Daphnia* average length.

peated itself, resulting in the population growth observed from October 14 to 17.

PHYTOPLANKTON AND ZOOPLANKTON PRODUCTION

If the above hypothesis is correct, the value of the various rates affecting the size of the standing crop should be amenable to calculation if the necessary data are available.

The measurement of productivity involves the following three fundamental concepts (Clarke 1946):

Standing Crop—the amount of organisms existing in the area at the time of observation.

Material Removed—the amount of organisms removed from the area per unit time.

Production Rate—the amount of organisms formed within the area per unit time.

The rate of change of standing crop may be expressed in terms of a simple differential equation in which

$$\frac{dP}{dt} = P(A - R - L) \qquad (1)$$

the rate of change of the crop P in respect to time $\frac{dP}{dt}$ is determined by the difference between the rate of assimilation (A) per unit crop and the sum of the rate of respiration (R) per unit crop and the rate of loss (L) per unit crop.

Ideally the crop P_t after time t resulting from initial population P_0 could be determined by integration of the above equation yielding:

$$P_t = P_0 e^{(A-R-L)t} \qquad (2)$$

In natural situations, A, R, and L vary as a result of environmental change, hence these rates have to be estimated at short-time intervals and average values obtained. The amount of material formed or lost can be expressed as the product of the average rate of change of standing crop times the average standing crop during the period of time selected. The value of the standing crop P_t will be given by the equation

$$P_t = P_0 - \bar{P}\,(A - \bar{R} - \bar{L})t \qquad (3)$$

Although this theory is simple, the determination of the values of P, A, and L in terms of the same unit is difficult and sometimes impossible. The values of these items computed by the following methods are given in Table 2.

Phytoplankton standing crop. The average standing crop of phytoplankton based on chlorophyll concentration and expressed as mg ash-free dry weight/L is given in Column 1 of Table 2 for the various sampling dates.

Gross production rate. The average rate of photosynthesis as measured in clear bottles corrected for black-bottle respiration was taken as the rate of gross production of phytoplankton (Column 2, Table 2). It was assumed that one μmole O_2 is equivalent to 30 μg glucose, and that photosynthesis occurred at the average rate for 12 hours. Gross production averaged 0.869 mg glucose/mg ash-free dry weight/day during September and 0.512 for October.

The average amount of glucose produced/L/day is given in Column 7. The figures were obtained by multiplying the average gross production rates by the appropriate values of standing crop.

Net production rate. Unfortunately one cannot obtain a direct measurement of phytoplankton respiration from black-bottle oxygen consumption data since phytoplankton, zooplankton, and bacterial respiration are included in these. An estimate has been made of phytoplankton respiration

TABLE 2. *Calculations of phytoplankton and zooplankton productivity*

Dates	1 Phyto-plankton standing crop	2 Gross production rate	3 Net production rate	4 Rate of change of phyto-plankton	5 Rate of phyto-plankton loss	6 Zoo-plankton standing crop	7 Gross production	8 Net production	9 Grazing loss	10 Zoo-plankton respiration	11 Net zoo-plankton production	12 Zoo-plankton assimilation
9/6–9/8	.699	.756	.626	+.448	.178	.220	.528	.438	.163	.101	.124	.225
9/8–9/11	.898	.765	.635	−.085	.720	.480	.687	.570	.459	.220	.091	.311
9/11–9/17	.624	1.062	.932	−.085	1.017	.834	.663	.582	.553	.382	.072	.454
9/17–9–22	.383	.882	.752	−.084	.836	.857	.338	.288	.349	.393	—	.393
9/22–9/26	.571	.909	.779	+.236	.543	.663	.519	.445	.403	.304	—	.304
9/26–9/30	.700	.847	.717	−.100	.817	.470	.593	.502	.350	.215	—	.215
9/30–10/3	.588	.878	.747	+.032	.715	.206	.516	.439	.129	.094	—	.094
10/3–10/7	.532	.780	.650	−.079	.729	.112	.415	.346	.063	.051	—	.051
10/7–10/14	.488	.377	.247	.000	.247	.081	.169	.111	.039	.037	—	.037
10/14–10/17	.532	.243	.113	+.105	.008	.106	.129	.060	.060	.049	.021	.070

Units of Measurement:
Column 1—mg ash-free dry wt/L.
Column 2–5—mg glucose/mg ash-free dry wt/day.
Column 6—mg dry wt/L.
Column 7–12—mg glucose/L/day.

during the summer of 1957 by measuring oxygen uptake of net concentrates of phytoplankton taken when zooplankton was low in number. The concentrates were kept in black-bottles for a period of six hours. The average value of respiration obtained from a series of 26 samples was 0.036 μmole O_2/μg chlorophyll/hour, or 0.130 mg glucose/mg ash-free dry weight/day. This figure may be regarded as a maximal value since it obviously includes some contributions from zooplankton respiration. Riley (1941a) presents a figure of similar magnitude for summer respiration of phytoplankton in Long Island Sound (0.110 mg carbon/mg phytoplankton carbon/day).

The average net production rates (Column 3) were computed by subtracting 0.130 from each of the values of average gross production. Net production/L/day is given in Column 8.

Rate of phytoplankton loss. The average rate of loss was determined by subtracting the average rate of change of phytoplankton from average net production. The rate of change of phytoplankton was calculated by dividing the difference between population values on two successive dates by the number of days between dates and then dividing this quotient by the average population for the two dates (Column 4).

Average daily rate of loss expressed as mg glucose/mg ash-free dry weight/day is entered in Column 5.

Grazing loss. The average zooplankton standing crop (mg/L) is entered in Column 6. An excellent correlation (r = .969) occurs between average zooplankton and average rate of loss of phytoplankton for those dates (September 6–26) when turbulence was not believed to be a factor causing major losses (Fig. 3). The average ratio of the rate of phytoplankton loss to zooplankton during this period was 1.064, which indicates that one mg of zooplankton will filter 1.064 liters of water per day.

Since most of the zooplankton was *Daphnia*, comparison of the calculated grazing rate with Ryther's (1954) data on the filtering rate of *Daphnia magna* would provide a check on the validity of the grazing coefficient. Ryther found a straight line relationship when food consumption/mg dry weight of *Daphnia* was plotted against size of *Daphnia* (mg dry weight/individual). Maximum food consumption per animal, however, occurred in animals with a dry weight of 0.11–0.12 mg, and the maximum filtering rate of animals of this size was 81 ml/animal/24 hours, which would be 0.736 L/mg dry weight/day. The average weight of *Daphnia* in Canyon Ferry Reservoir was 0.037 mg/animal. According to Ryther's curve (Figure 1 of his paper) animals of 0.04 mg size were filtering *Chlorella* at the rate of 3.6 million cells/mg dry weight/hour; whereas, the animals of size 0.11 mg were filtering at the rate of 2.5 million cells/mg dry weight/hour. The filtering rate for animals weighing 0.04 mg would be $3.6/2.5 \times 0.736 = 1.060$ L/mg/day which compares very favorably with the estimate of 1.064.

Zooplankton assimilation and respiration. Another estimate of the validity of the grazing coefficient can be made if the assimilation of the zooplankton is known, since the organic material obtained by grazing must at least equal assimilation, assuming 100% digestion efficiency.

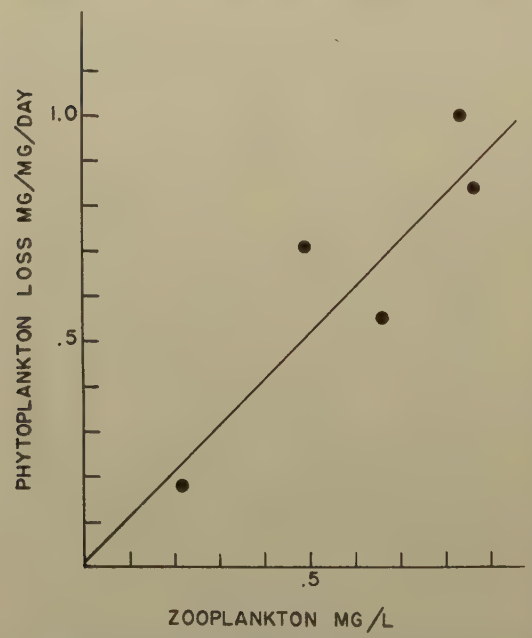

FIG. 3. Loss of euphotic zone phytoplankton plotted against zooplankton population.

A series of 29 respiration measurements of *Daphnia pulex* and *Daphnia longispina* were made at water temperatures comparable to those of the euphotic zone during this study. The average was 0.636 μmole CO_2/mg dry weight/hour, which is equivalent to a daily rate of glucose consumption of 0.458 mg/mg dry weight. Zooplankton respiration has been calculated on the basis of this factor, and the results are entered in Column 10 of Table 2 as mg glucose/L/day.

In Column 9, the grazing losses/L/day are entered. These values were derived by multiplying the weight of the average zooplankton standing crop by 1.064 times the weight of the average phytoplankton standing crop. It will be noted that the values of the amount of material grazed exceed zooplankton respiration except during the time when the zooplankton population was at a maximum (September 17–22). This indicates that the maximum zooplankton population was not obtaining sufficient food to maintain its respiratory demand, which inevitably led to a decline in the population.

The increase in standing crop of zooplankton (Column 11) must be added to the respiration values in order to obtain a measure of total material assimilated. The sum of respiration and increase in standing crop are shown in Column 12. The average of all values of assimilation was 0.216 mg glucose/L/day compared to an average value of grazing of 0.255 mg glucose/L/day. This indicates a digestive efficiency of 85%, which compares favorably with Conover's (1956) estimate of 80% for *Acartia clausi*.

A logical inference from the above statement is that bacterial respiration should be high during periods of zooplankton population growth, since the phytoplankton which is not assimilated would be excreted as feces and subject to bacterial decay. If this is so, then a high correlation should exist between zooplankton grazing and black-bottle respiration. In Figure 4 average daily phytoplankton consumption by the grazing of zooplankton is plotted against the corresponding values of black-bottle respiration (September 6–October 14). The correlation coefficient obtained (r = .978) is highly significant.

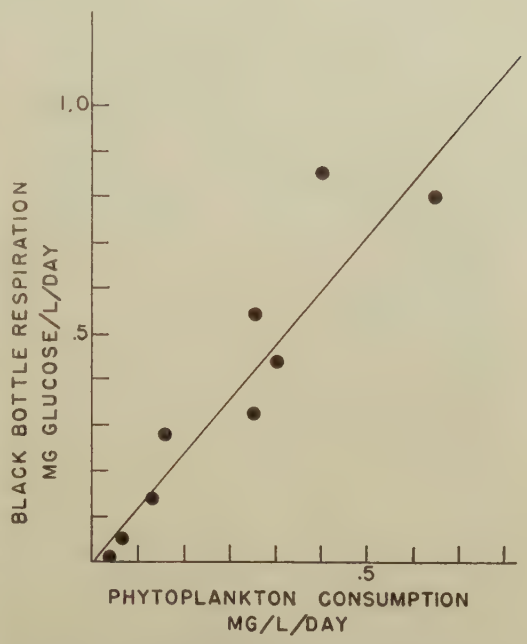

FIG. 4. Calculated average daily grazing consumption of phytoplankton plotted against average daily black-bottle respiration.

PRIMARY AND SECONDARY PRODUCTION

A balance sheet has been drawn up in Table 3 showing the calculated rates of production and consumption in the euphotic zone and consumption in the zone receiving less than one per cent light (dysphotic zone). The rates used in calculating the euphotic zone values are taken from the appropriate columns in Table 2. These values were converted to g glucose/m^3/day and multiplied by the number of days in the corresponding time period. The sum of the various values was then multiplied by the average depth of the euphotic zone (7.62 m) giving the amount produced or consumed as g glucose/m^2. The dysphotic zone data were based on the average of the populations present in the various depth zones. These values were converted to g/m^2 by multiplying them by the average depth of the dysphotic zone (14.9 m) times the number of days (41).

Gross primary production amounted to

TABLE 3. *Production and consumption of glucose from September 6–October 17, 1957*

	g glucose/m²
Euphotic Zone	
Gross production	137.2
Phytoplankton respiration	23.2
Net production	114.0
Grazing loss	82.8
Zooplankton respiration	61.6
Zooplankton net production	7.8
Increase in phytoplankton crop	1.8
Loss to dysphotic zone	29.4
Dysphotic Zone	
Zooplankton respiration	25.7
Net zooplankton production	2.2
Increase in phytoplankton crop	4.4
Total dysphotic zone	32.3

137.2 g glucose/m². Net primary production amounted to 114.0, and phytoplankton respiration was 23.2 g glucose/m². The computed amount of grazing loss was 82.8 and increase in phytoplankton standing crop 1.8, leaving a balance of 29.4 g glucose/m² which represents loss to the dysphotic zone.

In the dysphotic zone zooplankton respiration was calculated to be 25.7 and net zooplankton production 2.2, or a total zooplankton assimilation of 27.9 g glucose/m². The increase in phytoplankton in the dysphotic zone amounted to 4.4 g glucose/m². Total consumption would be 32.3 which is slightly more than the estimated loss from the euphotic zone. Considering the numerous sources of error, the agreement between the two calculations is probably as good as can be expected.

The sum of zooplankton assimilation in both zones is 97.3 g glucose/m², which is 85 % of net primary production. Since the total increase in phytoplankton crop was 6.2, only 10.5 g glucose/m² can be assigned to bacterial, microzooplankton, and bottom fauna consumption. This estimate does not appear unrealistic since no large insect emergences were noted during 1956–1957. Furthermore, stomach analyses of the rainbow trout, which is the principal game fish item, reveal that *Daphnia* is practically the sole food of these fish (Graham 1956).

The ratio of zooplankton net production to zooplankton assimilation 10.3/97.3 is 10.5 %, which is of the same order of magnitude as other estimates of efficiency in inland lakes (Lindeman 1942, Juday 1940).

SUMMARY

The standing crop of euphotic zone phytoplankton in Canyon Ferry Reservoir during September and October 1956 was considered in relation to photosynthesis, respiration, zooplankton, and turbulence. Loss of phytoplankton from the euphotic zone correlated well with zooplankton during September and with turbulence during late September and October.

On the basis of measurements in phytoplankton standing crop, net photosynthesis, and zooplankton standing crop, a grazing coefficient was computed (G = 1.064 L water/mg dry weight zooplankton/day). On the basis of this coefficient, loss of phytoplankton due to zooplankton grazing was computed. The average value of grazing loss of phytoplankton was 0.255 mg/L/day. On the basis of measurements of respiration of *Daphnia* and net production of zooplankton, an estimate of zooplankton assimilation was made. The average value was 0.216 mg/L/day, which indicates a digestion efficiency of 85 %.

An estimate of the amount of loss from the euphotic zone to the dysphotic zone was made from data on average net production, grazing loss, and net increase of euphotic zone phytoplankton. This amounted to 29.4 g/m² during the 41-day period of study. An estimate of dysphotic zone consumption was made on the basis of zooplankton assimilation and net increase in phytoplankton in this zone. This amounted to 32.3 g/m², which is similar in magnitude to the estimated loss from the euphotic zone.

Total gross and net primary production amounted to 137.2 and 114.0 g glucose/m², respectively. Zooplankton assimilation (97.3 g glucose/m²) amounted to 85 % of net primary production. The ratio of zooplankton net production to zooplankton assimilation was 10.5 %.

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A Comparison of Drogue and GEK Measurements in Deep Water[1]

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ABSTRACT

Two series of current measurements made with GEK and drogues are shown to agree closely, not only in the averaged results of three days' data, but in short-period variations about the mean. The variations measured are probably too large to be the ordinary tide, and the possibility of their being the orbital velocities of internal waves is discussed.

INTRODUCTION

The GEK (Geomagnetic Electrokinetograph, von Arx 1950) has been used extensively in studying the California Current. The accuracy of an average of GEK measurements over several hours in weak currents has been discussed (Knauss and Reid 1957). The validity of individual GEK measurements in a weak current system with large fluctuations in velocity has yet to be demonstrated in deep water. Von Arx (1950) has compared serial GEK measurements in the shallow water of Georges Bank with predicted tidal currents. He has used the results to estimate the effect of the conductivity of the bottom in measurements of shallow currents which extend to the bottom. Vaux (1955) has continued this work in the English Channel, comparing his GEK measurements with The Admiralty Tidal Stream data and the set of the ship as determined by the Decca Navigator system. He has derived a correction factor for use in that particular shallow (30 m) area of the English Channel, but notes that further work is needed in the velocity range below one knot.

The currents off California are slow, rarely exceeding a knot. Most of the GEK measurements fall below 30 cm/sec. Such currents are difficult to measure by GEK and not easy by any other means. The author has tried at various times to compare the results of dynamic height computations in this region with the drift of drogues. On several of these occasions the GEK has been used. It is the results of one of these attempts which allow the drogue and GEK results to be compared in total drift and variation about the mean.

THE DATA

In January of 1952 a drogue was put out in the deep water between Santa Catalina and San Clemente Islands, off California (Fig. 1), and followed for about 66 hours, at which time it was close to Catalina and its movement had almost stopped. It was recovered and set out again and followed for about 69 hours. During the tracking, GEK measurements were made around the drogue, and frequent fixes were made of its position both by bearings on the islands and by radar ranges. From their successive changes one would estimate the greatest inaccuracy of the positions to be about a quarter mile when the drogue was between the islands and about a half mile as it moved south of San Clemente Island (Figs. 2 and 3). The drogue consisted of an 8×8 feet biplane of canvas on a metal frame suspended below a float. The float reached about 8 inches above the water. A light

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The author is indebted to Mr. James Snodgrass for a device for maintaining contact with the drogue and measuring its distance from the vessel, and to Captain E. E. Mitchell and the crew of the California Division of Fish and Game vessel Yellowfin, aboard which this work was done.

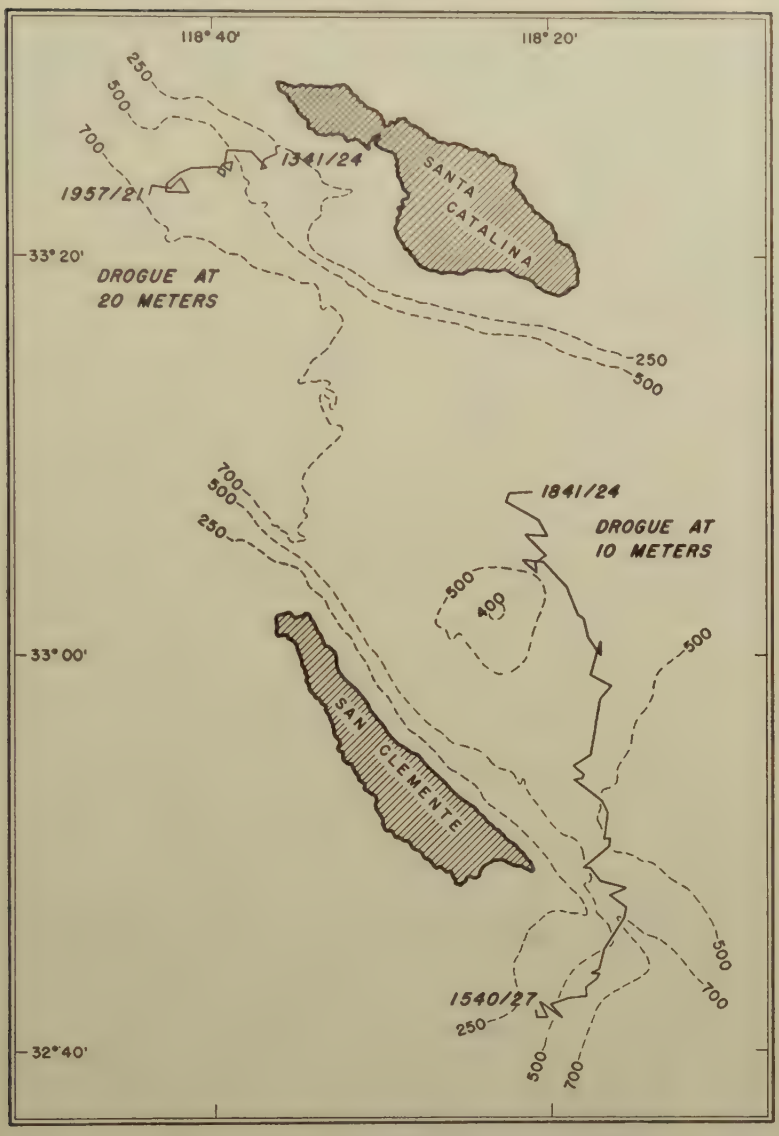

FIG. 1. Trajectories of drogues, January 1952.

on a slender bamboo pole reached 6 feet above the float. Flags and radar targets were omitted to reduce wind effect.

The two observed drogue trajectories and the trajectories obtained by integrating the GEK measurements are shown by Figures 2 and 3. The depth of the thermocline and the east component of the current measured by the GEK are shown by Figure 4. In the first series there was a fairly readable thermocline. In the second the thermocline was hard to locate and the bathythermograph instrument began to give erratic surface values. The second set of thermocline measurements may be seriously in error and will not be discussed further.

THE RESULTS

The velocities measured by the GEK were corrected for the electrode-droop (Knauss and Reid 1957) and compared with the movement of the drogue. In the first case the drogue moved with an average velocity of 5.7 cm/sec, while the average of the GEK

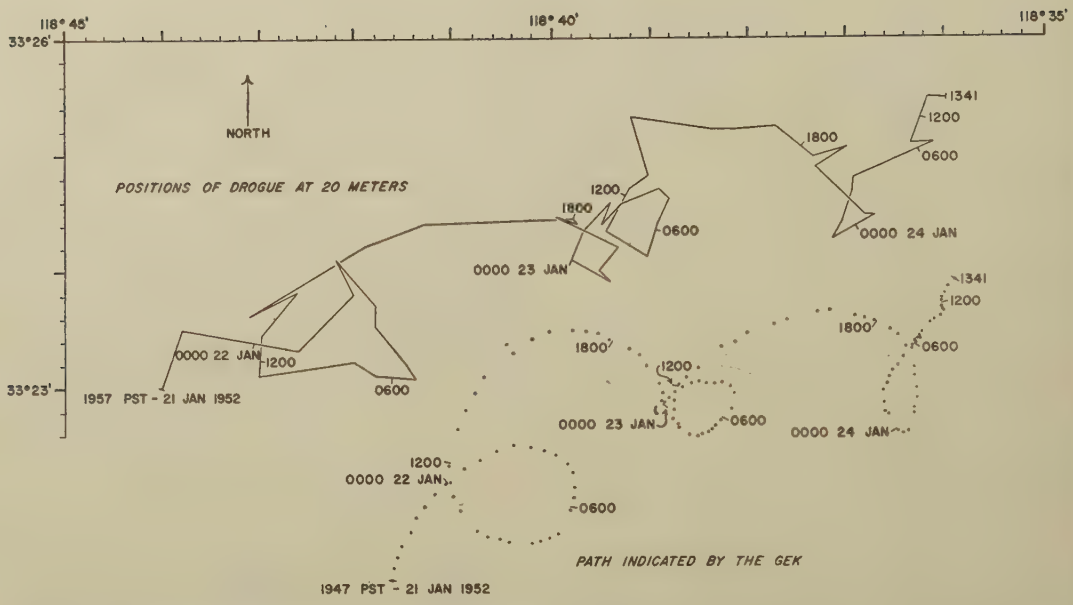

FIG. 2. Trajectory of drogue near Santa Catalina Island and path indicated by the integrated GEK measurements of velocity. (Starting points offset to avoid overlap.)

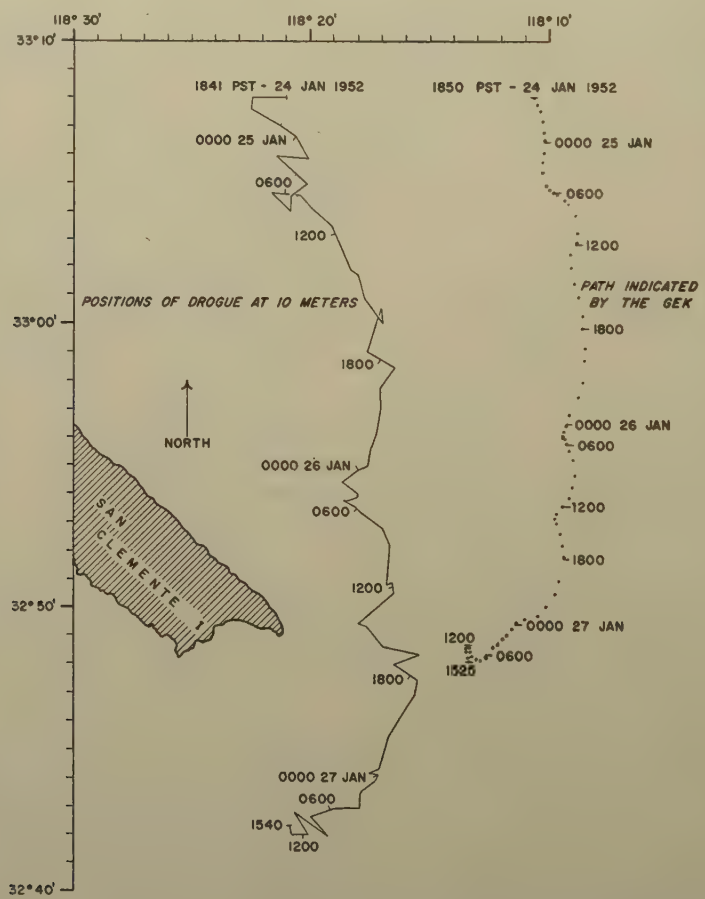

FIG. 3. Trajectory of drogue near San Clemente Island and path indicated by the integrated GEK measurements of velocity. (Starting points offset to avoid overlap.)

measurements was 4.1 cm/sec. In the second case the drogue's average velocity was 19.3 cm/sec, while the GEK averaged 14.6 cm/sec.

The principal result of these measurements is that the GEK measurements are shown to agree closely with the drogue movement. This is true not only in total drift but in the time variations about the mean (Figs. 2, 3). On previous trials of short time-series (24 hours) with the GEK, fluctuations of the order of 12-hour period and 10 to 20 cm/sec amplitude had been seen, but it was not possible from such scanty data to call these tidal fluctuations nor even accept them as real motion. (Longuet-Higgins *et al.*, 1954, state that the natural earth-current potentials associated with geomagnetic disturbances which have been observed on land may result in a daily variation of perhaps ¼ knot if they obtain in the ocean also.)

Longer series of bathythermograph measurements (6 days) had shown semidiurnal internal waves in the region (Reid 1956). Therefore the depth of thermocline was compared (Fig. 4) with the height of tide at the coast, and the east component of current (GEK) with the rate of change of the tidal height (as a rough indication of the shape of the tidal transport current).

The two series are not long enough to confirm the tidal periodicities, but the segments show enough similarity to justify the hypothesis that they are there. (The inertial period at this latitude is 22 hours, and of course cannot be distinguished from a diurnal tide in these few data. It is the semidiurnal part which we shall discuss.) Remembering that these are not measurements made at one position but following a drogue in water of varying depth (and, in the first case, up against a barrier), a central section of 24 hours has been chosen for analysis. The 24-hourly running mean has been subtracted from the GEK data and the latitude and longitude measurements. Then curves of 24- and 12-hour periods were fitted to the north and east components of the GEK, the positions north and east, and the depth of the thermocline. (Since the variations of latitude and longitude will be the integral of the velocity components, the positions have been analysed accordingly to compare with the GEK results.) The results of analysis of the 24 hours beginning 1400 PST 22 January 1952 are given in Table 1.

Comparing the results from drogue and GEK, the differences in amplitudes (especially in the semidiurnal) are not significant. This was to be expected from Figures 2 and 3.

The likelihood that these are tidal fluctuations can be tested in certain ways for obvious contradications. As models one can take the simple cases of one- and two-layer systems.

I. *The one-layer system.* If the observed oscillation in the current is the tide, the

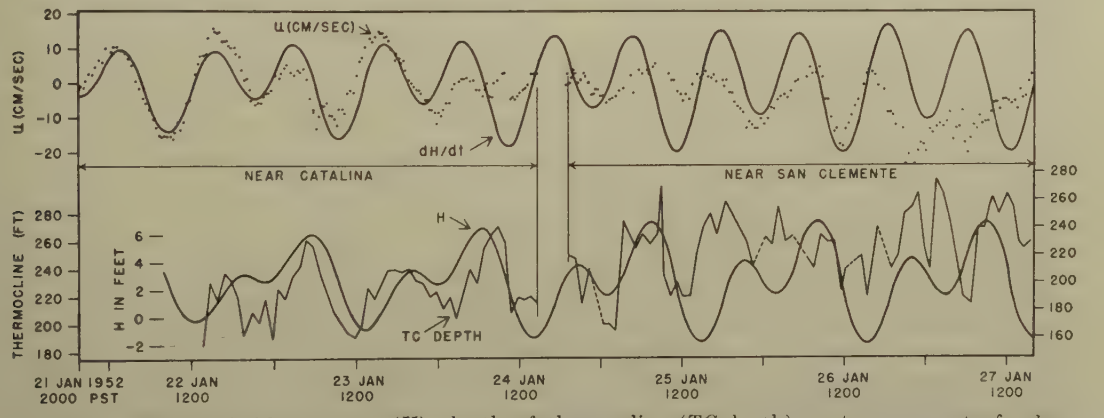

FIG. 4. Height of tide at coast (H), depth of thermocline (TC depth), east component of velocity measured by GEK (u), and rate of tidal rise (dH/dt). Scale for dH/dt is arbitrary and not shown.

TABLE 1. *Results of diurnal and semidiurnal analysis of 24 hours of data beginning 1400 PST 22 January 1952*

	Data	Diurnal		Semidiurnal	
		Amplitude cm/sec	Phase	Amplitude cm/sec	Phase
GEK	North component	4.5	114°	7.8	120°
	East component	6.8	39°	7.8	44°
Drogue	North component	3.3	107°	6.6	99°
	East component	11.1	39°	8.8	17°
	Depth of thermocline	3.1m	62°	6.4m	185°

water should move in its forward cycle a distance of

$$S_1 = \int_{-\pi/2m}^{\pi/2m} u \cos mt \, dt = \frac{2u}{m},$$

where u is the amplitude of the onshore current and m the frequency. If the current extends to the bottom in depth h, then the resulting rise in the height of the tide S_2 will be given by

$$S_1 h = S_2 l,$$

where l is the distance to the mainland. Using the observed value for the semidiurnal wave, $u = 7$ cm/sec, $m = 2\pi/12$ hr, $h = 1$ km, and $l = 60$ km. Total forward movement would be 1 km, and the rise in tide would be 17 m, which is about ten times too large.

Thus the currents either do not extend to the bottom or else do not obtain over a large area.

Since the oscillations were shown by the GEK as well as the drogue, a qualitative treatment by Longuet-Higgins *et al.* (1954) shows that either the velocity varies with depth or the "conductivity" of the sea bed is high. If the stream extends uniformly to the bottom, is long and straight, and the "conductivity" of the sea bed is low, the towed electrodes will record no signal. If the "conductivity" is high then the potential gradient is small and the current density at the sea surface (which is measured by the towed electrodes) will depend only upon the surface velocity. If the "conductivity" is high, $\frac{\rho D}{\rho' h} \gg 1$, where ρ and ρ' are the resistivity of the water and the sea bed, respectively, h the depth, and D the width of the current. Taking $\rho = 25$ and $\rho' = 2 \times 10^4$ ohm-cm, $h = 1$ km, $D \gg \frac{\rho' h}{\rho}$, or 800 km. This is perhaps the right order for a tidal wave, but the velocities have already been shown to be too high. The GEK disposes, in addition, of the possibility that the current extends to the bottom but is narrow.

II. *The two-layer system.* A very interesting possibility is that these currents are the orbital velocities of internal waves of tidal period. The data can be inserted in the two equations

$$c^2 = \left(\frac{\omega^2}{\omega^2 - \lambda^2}\right)\left(\frac{gh'h''}{h' + h''}\right)\left(1 - \frac{\rho'}{\rho''}\right),$$

and

$$u = \frac{-c\zeta}{h'},$$

where c is the phase velocity, u the amplitude of orbital velocity, ω the frequency, λ the Coriolis term, g the gravity term, h' and h'' the thickness of upper and lower layers, respectively, ρ' and ρ'' the density in upper and lower layers, respectively, and ζ the amplitude of rise and fall of interface. The first is the expression for an internal wave in a two-layer system on a rotating earth (Haurwitz 1950). The second derives from continuity. From the measured quantities, assuming a semidiurnal wave, u is 7.8 cm/sec, h' and h'' are 69 and 1000 m, $(1 - \frac{\rho'}{\rho''})$ is 4×10^{-3} (taking ρ'' as the mean density below the thermocline), and ζ is 6.4 m.

The first equation gives $c = 1.6$ m/sec and the second gives 0.84 m/sec. These are at least of the same order when the limitations of measurement and of the two-layer system are considered.

Longuet-Higgins *et al.* (1954) show qualitatively that if the velocity varies with depth and the "conductivity" is high, the

electrodes will measure a current density which depends only upon surface current. If the values of phase velocity computed in the preceding paragraph are of the right order then $D \ll 800$ km, and the "conductivity" is almost certain to be low.

If the "conductivity" is low the towed electrodes will measure (approximately) the difference between the surface velocity and the mean velocity. In a two-layer system $u_1 h_1 = u_2 h_2$, where u_1, u_2 and h_1, h_2 are the velocities and depths of the upper and lower layers, respectively. Taking h_1 and h_2 as 69 and 1000 m

$$u_1 - u_2 = u_1\left(1 - \frac{h_1}{h_2}\right) \sim u_1$$

and the signal measured by the electrodes depends almost entirely upon the surface current.

CONCLUSION

A close agreement has been found between individual GEK measurements and the movement of a drogue in a system whose velocity varied with time. Variations of a similar order had been shown in the California Current by the GEK. Because of the possibility that these variations were geomagnetic disturbances rather than water motion, the measurements described in this paper were made. The results imply that the variations represent real water motion. In the California Current the variations in surface velocity are of the same order of magnitude as the mean.

In these data the time variation of current strongly resembles the tide. The observed current was too strong to be the orbital velocity of a wave extending to the bottom over a large area. But the GEK will not measure a current extending to the bottom which does not cover a large area. Therefore the current measured at the surface did not extend to the bottom.

In the equations of a semidiurnal internal wave phase, velocity can be computed both from the density distribution and from the observed motion at the surface and the interface. The observed quantities give results which are not contradictory.

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The Chaetognatha of the Inshore Waters of North Carolina[1]

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ABSTRACT

Plankton samples were taken along the coast and in the sounds of North Carolina to determine the inshore distribution of the Chaetognatha. Five species were found within ten miles of the coast. The large northern sounds with water of reduced salinity do not appear to support an appreciable chaetognath population. *Sagitta hispida* and *S. tenuis*, the two characteristic inshore species, were common in the small bays and sounds south of Pamlico. Cape Hatteras with the colder Virginian water to the north appears to be a barrier to the northward occurrence of *S. hispida*. A more concentrated population of chaetognaths was found inshore than collections made a few years earlier indicated for the offshore waters. The same five species were also found along the west coast of Florida in an earlier study.

INTRODUCTION

On earlier cruises of the Albatross III of the U. S. Fish and Wildlife Service, and of the Atlantis and Caryn of the Woods Hole Oceanographic Institution, many plankton samples were collected from the waters over the continental shelf off North Carolina and in the Florida Current beyond. The chaetognaths in these samples have been studied and their abundance and relationships to the hydrography discussed (Pierce 1953, Bumpus and Pierce 1955). Because of the size of the vessels mentioned almost all these samples were taken 10 or more miles from shore. It was with interest, therefore, that I took the opportunity to collect plankton along the coast and in the sounds of North Carolina during the summer of 1956.

METHODS

These samples were collected with two types of plankton nets. The larger was a half-meter net with No. 0 mesh (15 openings/cm) and the smaller was a Clarke-Bumpus quantitative net with No. 2 mesh (21 openings/cm). The rather coarse mesh of both nets allowed rapid filtering of the water. Oblique tows were made from near the bottom to the surface and for a period of ten minutes as a rule. During this time from three to ten cubic meters of water were usually sampled in the Clarke-Bumpus sampler. Much more was filtered in the half-meter net.

Salinity was determined with a set of sea water hydrometers. A number of samples were titrated with silver nitrate standardized against standard sea water as a check. The hydrometer readings agreed within $\pm 0.2‰$ with the titrations. Water temperatures were taken with a simplified reversing thermometer with an accuracy of $\pm 0.1°C$.

AREA STUDIED

The chaetognaths were sampled from a narrow strip of coastline extending from Oregon Inlet on the north to Shallote Inlet to the south (Fig. 1). The former is above Cape Hatteras and within 50 miles of the Virginia border while the latter is within 10 miles of South Carolina. The Carolina coast is bordered by offshore bars which form many shallow sounds. These sounds diminish in size towards the south and disappear below Cape Fear.

During the period of sampling the salinity

[1] The author wishes to express his appreciation for the use of the facilities of the Duke Marine Laboratory during the summer of 1956. He is indebted to the National Science Foundation for a grant which facilitated this work. The Department of Conservation of the State of North Carolina and the University of North Carolina Institute of Fisheries Research allowed him the use of their boats and equipment. Dr. Gerald Posner of the latter institution was especially helpful in titrating a number of salinity samples and helping with the collection of several plankton samples.

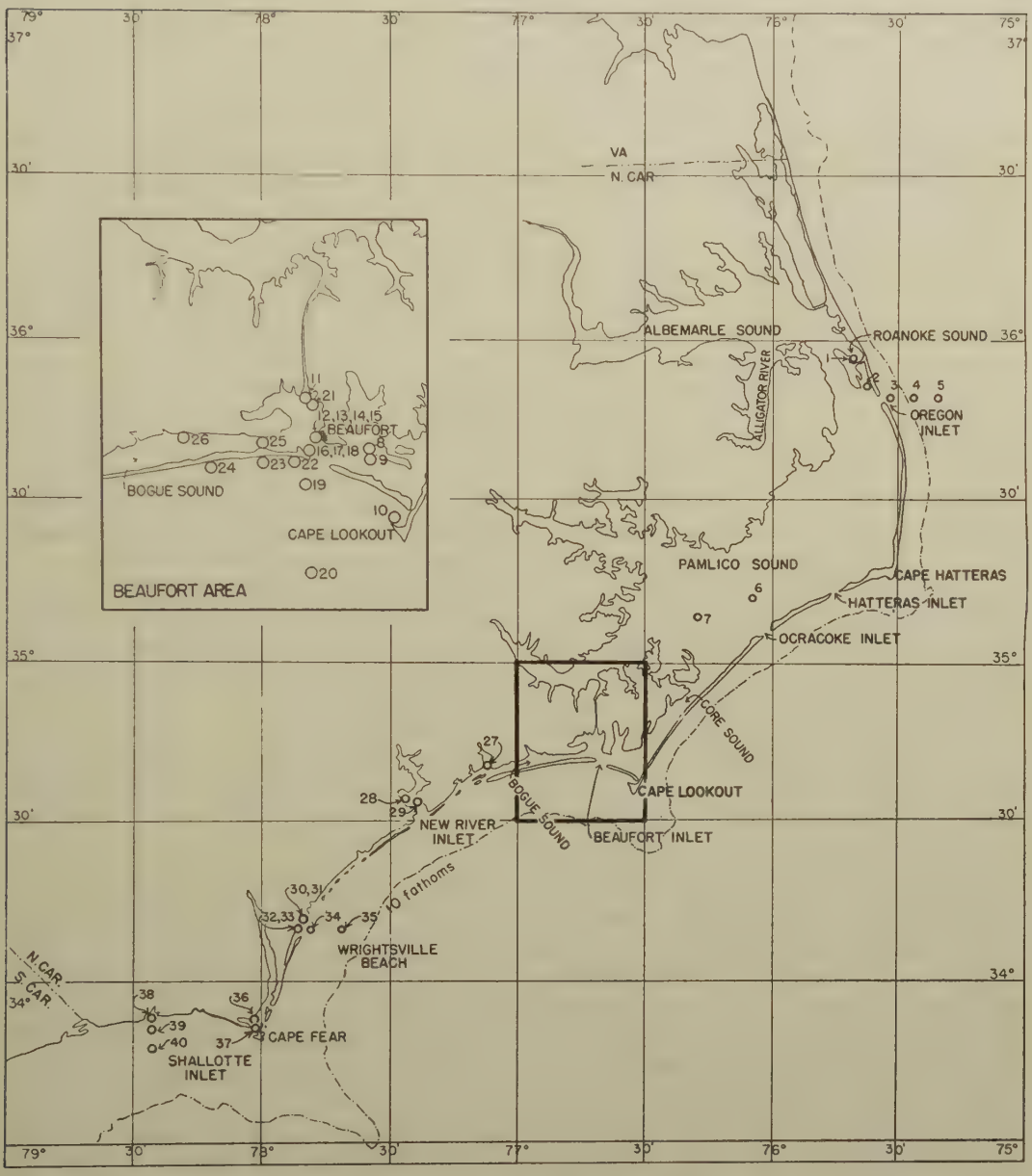

FIG. 1. Collecting stations along the coast of North Carolina. The insert is an enlargement of the Beaufort area (rectangle in heavy lines).

in the sounds showed a gradient from north to south. Albermarle Sound in the north may be considered essentially a body of fresh water except at its entrance where salinities of 6–8‰ have been found (Marshall 1951). In Roanoke Sound the salinity at two points was 12.5 and 13.5‰. Except in the mouth of the Cape Fear River, opposite Battery Island, where the salinity varied from 29.6 to 31.4‰, all the remainder of the samples in the sounds and inlets south of Pamlico were above 34‰. The decreasing drainage and smaller size of the sounds from the north to the south are the principal factors influencing the salinity gradient.

Plankton and salinity samples were taken

outside the sounds at Oregon Inlet, Beaufort Inlet, Wrightsville Beach, and at Shallote Inlet near the Carolina border. The salinity six miles east of Oregon Inlet was 30.3‰ on the surface and 33.2‰ at 60 feet. At the remaining points offshore the salinity was above 34.4‰ and usually above 35‰ even when close to shore.

Surface water temperatures were taken at almost every station. In the inshore water north of Cape Hatteras they ranged from 21.4 to 22.7°C. Below the Cape the temperature range was from 26.2 to 29.6°C. Except for the colder water north of Cape Hatteras no influence of temperature on the distribution of the chaetognaths was evident. In order to compress the tabular material, detailed temperature data have been omitted.

OCCURRENCE OF CHAETOGNATHS

Five species of chaetognaths were collected in the inshore waters (Table 1). These were: *Sagitta hispida*, *S. tenuis*, *S. helenae*, *S. enflata*, and *Krohnitta pacifica*. The two commonest species were *S. hispida* and *S. tenuis*, both occurring abundantly in the sounds and inlets. In parts of the sounds some distance from their channels into the Atlantic *S. hispida* was usually the most abundant. This was true for parts of Beaufort Inlet, Core Creek, and Bogue Sounds. In the inlets proper and a few miles beyond in the Atlantic *S. tenuis* was usually the most abundant. This was very noticeable in a series of samples taken from Beaufort and Oregon Inlets and Wrightsville Beach into the Atlantic. Conant (1895) first described *S. hispida* from Beaufort, N. C. The next year (1896) he described *S. tenuis* from Jamaica; but he never recorded this species from the Beaufort area where it is now common.

TABLE 1. *Collections of chaetognaths along the Coast of North Carolina*

Species	Range of surface salinity ‰	Map station
None	12.5 to 22.3	1, 2, 6, 7
S. hispida	29.6 to 36.0	8 to 19, 21 to 30, 32, 33, 37, 39, 40
S. tenuis	22.7 to 36.0	3, 4, 5, 8 to 40
S. helenae	32.6 to 35.9	5, 19, 20, 35
S. enflata	30.3 to 35.9	4, 5, 19, 35
K. pacifica	32.6 to 35.9	5, 20, 30, 35

In the samples collected five or more miles from shore *S. tenuis*, *S. enflata*, *S. helenae*, and occasionally *K. pacifica* occurred. With but one exception off Shallote Inlet, *S. hispida* was not found this far offshore.

In Roanoke Sound and Pamlico Sound, where the salinity was reduced, no chaetognaths were collected. Although samples were not obtained from Albermarle Sound it is doubtful, with the reduced salinity reported from there, if there would be any chaetognaths present in that area. No large chaetognaths were present in several additional samples from Pamlico Sound loaned by the Institute of Fisheries Research. Only a very few minute forms several millimeters long which were too small to identify specifically were in these samples. It appears that the northern sounds with their reduced salinity lack any appreciable chaetognath population over most of their area.

Just outside the mouth of Oregon Inlet (Station 3) 19 *S. tenuis* were caught, and 6 miles east of this inlet 4 *S. tenuis* and 6 *S. enflata* were found. Eleven miles east of the inlet 24 *S. tenuis*, 10 *S. enflata*, 8 *S. helenae*, and 1 *K. pacifica* were taken. Just above the Cape much colder Virginian water (Bumpus and Pierce 1955) is encountered, while below the Cape warmer Carolinian water is found These results support the theory that Hatteras acts as a barrier to the northward distribution of *S. hispida*. *S. tenuis* extends farther north along the coast.

Animals which live in the Florida current can easily pass Hatteras farther offshore near the edge of the shelf. However, not all of these forms seem to be able to overwinter in the shallower shelf water north of Hatteras, and as a result the Cape is an effective barrier to some inshore animals. It is of course not the Cape itself which is the primary barrier but the colder Virginian water which is contained to the north by the prominence of the Cape.

Bumpus and Pierce (1955) recorded *S. enflata*, *S. helenae*, *S. hispida*, *S. minima*, *S. serratodentata*, and *S. tenuis* from samples

taken offshore in Carolinian type water. K. *pacifica*, found in this study, should be added to this list. This species may have been missed in the earlier work because of the smaller size of the samples taken with the Clarke-Bumpus sampler. The absence of *S. minima* and *S. serratodentata* from this present collection support the earlier findings that these two species are not common in the inshore water in this region.

ABUNDANCE

Fourteen quantitative samples were taken at different points along the coast (Table 2). In these samples *S. hispida* and *S. tenuis* were the most abundant inshore species. On a number of occasions more than 5 individuals per cubic meter were caught. Near Beaufort Inlet quantities as great as 48, 52, and 122 per cubic meter were taken. These inshore waters contained a more concentrated population of chaetognaths as compared to the offshore samples of previous cruises (Bumpus and Pierce 1955). Very few of the offshore cruises had as many as 5 specimens per cubic meter, and most contained no more than one per cubic meter.

DISCUSSION

The two commonest species collected along the North Carolina coast were *S. hispida* and *S. tenuis*. The former was found in greatest numbers very close to land and was usually the most abundant chaetognath in semi-inclosed bodies of water. Both species were also found along the coast of Florida (Pierce 1951) where *S. hispida* was associated with very shallow water and with water of reduced salinity. Along the North Carolina coast the close association with the shallow water in the sounds still holds, but since most of the sound water where *S. hispida* was found had a sailinity of 35‰ and above, the relationship of this species there to lower salinity water was not evident. This is an inshore species and it may be useful as an indicator of sound and alongshore water. Specimens found many miles off the coast would indicate the offshore movement of coastal water.

In North Carolina *S. tenuis* was most closely associated with water of higher salinity along the coast. It was less numerous in the shallow sounds where its abundance in many cases can probably be attributed to the daily tidal influx of outside water. Along the west coast of Florida this species was found close to shore during the winter when salinities were usually 30‰ and above, but it was more numerous five or more miles from shore where the water was more saline.

TABLE 2. *Abundance (No./m³) of Chaetognaths*

Map station	Species				
	S. hispida	*S. tenuis*	*S. helenae*	*S. enflata*	*K. pacifica*
8	0.3	0.4	—	—	—
11	3.0	1.1	—	—	—
12	8.3	0.6	—	—	—
15	21.4	17.0	—	—	—
16	11.4	2.6	—	—	—
18	2.1	4.4	—	—	—
19	10.4	8.1	0.3	0.3	—
20	—	19.0	34.4	—	0.3
22	6.0	46.0	—	—	—
23	15.6	106.4	—	—	—
24	5.0	42.5	—	—	—
38	—	3.3	—	—	—
39	1.0	18.4	—	—	—
40	6.3	5.9	—	—	—

S. enflata, *S. helenae*, and *K. pacifica* were taken infrequently in the inshore sampling in this study. *S. enflata* is widely ranging and occurred most abundantly in the samples collected farthest from shore. It is not normally found in Virginian water. Its presence at Station 4 north of Cape Hatteras indicates the incursion of Florida Current water at that point. *S. helenae* was taken only once as near as two miles to the coast. It appears to be found principally in the normally saline shelf water. *K. pacifica* strays over the shelf and was taken in a few samples several miles from the coast. It is associated with the Florida Current water.

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Turbulence Spectrum Studies in the Sea with Hot Wires

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ABSTRACT

Turbulence measurements of scales as small as two inches have been made in the ocean with hot-wire equipment which was especially designed for use in sea water. Observations have been made of the variation of the turbulence spectrum over a tidal cycle in the Strait of Juan de Fuca and of the influence of an underwater obstacle in altering the spectral distribution. A preliminary experiment has been carried out to correlate velocity and pressure fluctuations due to turbulence in the ocean. From the work done to date the specifications for a hot-wire instrument for use in the sea can be outlined. A review of several types of turbulence measuring instruments that have been used in water is included.

INTRODUCTION

Although hot-wires have proved to be the best device for measuring turbulence in air they have not been developed to the point where they can be used to measure absolute values of the turbulent velocities in water over long periods of time. The main drawback to the use of hot-wires in water is the formation of a film on the wire which changes the wire characteristics so that it is difficult to obtain an absolute calibration of the system. A film will form even though the wire is used in filtered, distilled water. Under this circumstance a constant-current hot-wire system cannot be used to obtain useful information about the turbulent velocities. If, however, a constant-temperature system is used the usefulness of the hot-wire is increased markedly. The result of the formation of a film on the wire will be a decrease in the response of the constant-temperature system so that the small scales of turbulence will not be recorded after the wire has been in the water for some time. The larger turbulent scales will still affect the hot-wire until the film has become quite thick. If one is interested in determining the changes that occur in turbulent spectra the constant-temperature hot-wire will be quite adequate as long as the very small scale end is not important.

As there have been numerous difficulties in the development of suitable hot-wire equipment for use in water, a number of other methods have been developed to measure turbulent velocities. These methods include the use of thermistor, electromagnetic, and pressure measuring systems. It is the purpose of this report to review these different systems and to describe work with hot-wires which has been done at the Pacific Naval Laboratory.

THERMISTOR VELOMETER

Thermistors have been used extensively to measure temperature microstructure in the ocean, but they can also be used to measure average water velocities and turbulence. The thermistor velocity detector makes use of the fact that a heated body immersed in a flowing fluid will transfer heat to the fluid. If the detector is heated at a constant rate its final temperature will depend upon the velocity of the fluid. For a particular detector, heated at a constant rate, the velocity (U) of the fluid is related to the temperature difference (ΔT) between the unheated fluid and the thermistor by the relation

$$U = C/(\Delta T)^2$$

where C is a constant determined by the characteristics of the fluid and the detector. If the initial temperature of the detector is high enough, the variation in water temperature normally encountered in the ocean will have little effect on the accuracy of the measurements.

Misener (1954) describes a thermistor

velometer which is used essentially to measure average stream velocities from 0.1 to 4 M.P.H. The temperature sensing element is a small glass-encased bead thermistor (Western Electric Type 6014) with a resistance of approximately 10^5 ohms at 25°C. The heating element is wound on a thin-walled glass tube which is attached over the thermistor bead. The thermistor forms one arm of a Wheatstone bridge and the variation in thermistor resistance is reflected in a current change across the bridge. Because of the high resistance of the thermistor this current change will be nearly proportional to the temperature change in the detector, and therefore it is possible to convert current readings directly to temperatures and flow velocities.

For average flow velocities a meter is used across the bridge, while for turbulence measurements the thermistor bridge current can be recorded on film or by pen recorders. The limitation in the use of the thermistor velometer for the measurement of turbulent velocities is its response time. The detector response will be limited either by the response of the thermistor which is normally of the order of 1 to 2 seconds, or by the heat capacity of the heating element and its insulation. Some work has been done at the Pacific Naval Laboratory and at Scripps Institute of Oceanography (Snodgrass and Cawley 1957) to improve the response time of glass bead thermistors such as the Western Electric Type 6014. Techniques have been developed for grinding some of the glass from the thermistor bead and decreasing the response time to the order of $\frac{1}{10}$th of a second. The minimum turbulent scale size that can be measured with this time constant will depend on the average flow velocity past the detector.

ELECTROMAGNETIC FLOWMETERS

In his Bakerian Lecture of 1832 before the Royal Society, Faraday suggested that the laws of magnetic induction should apply to a stream of water, which is a conductor, moving through the earth's magnetic field. Faraday was unsuccessful in his attempt to measure the voltages produced in the River Thames at Waterloo Bridge. Since then there have been many successful measurements of tidal and stream currents using electromagnetic flowmeters. Longuet-Higgins (1949) gives a summary of the work of a number of observers.

The earlier measurements made use of submarine cables or fixed electrodes near the shores of channels or rivers (Cox 1956). Since 1946 a system known as the geomagnetic electro-kinetograph, which uses towed electrodes, has been developed in the United States (von Arx 1950). The potential difference developed between the silver/silver-chloride electrodes is of the order of 1 millivolt per knot. Towed electrodes have also been used in England for studying currents in the sea (Bowden 1953, Deacon 1955).

In order to reduce the size of the detecting equipment so that smaller scale fluctuations can be observed, a stronger magnetic field than the earth's must be produced. Instruments have been designed which use direct or alternating magnetic fields. Guelke and Schoute-Vanneck (1947) developed a detector designed for velocity measurements on the sea-bed. The unit consists of an exciting coil through which an alternating current is passed to produce the alternating magnetic field. The first experiments were carried out using an average vertical field of 15 gauss (compared to the earth's field which is less than one gauss) in the region between the silver electrodes. With the electrodes spaced 35.5 cm apart the induced motional e.m.f. was of the order of 270 microvolts per knot.

An electromagnetic flowmeter similar to the Guelke and Schoute-Vanneck instrument has been designed at the National Institute of Oceanography in England for measuring turbulence near the sea bed (Bowden 1955). The measuring head is 10 cm in diameter as compared to the 76 cm head of the Guelke and Schoute-Vanneck instrument, and the potential difference between the rhodium-plated electrodes was approximately 50 microvolts per knot. The measuring heads are attached to a tripod mounted on the sea bed, and a canvas fin attached to the vertical strut aligns the measuring heads into the flow. Bowden

and Fairbairn (1956) used this instrument to obtain measurements of Reynolds stresses in a tidal current. The average tidal velocity (U) during the measurements was 25 to 50 cm/sec, with the horizontal turbulent velocities (u) up to 10%U and the vertical turbulent velocities (w) up to 6%U. The frequency response of their electronics was flat below 1 cycle per second and fell to 50% at 9 cycles per second.

Grossman and Li (1956) have developed an electromagnetic flowmeter for turbulence investigations in pipe flow. A direct current electromagnet with 5.75-inch diameter pole pieces and a 2½-inch gap produced a maximum field intensity of about 9000 gauss which was practically uniform over the measuring region. One-, two-, or three-electrode probes with spacings as small as 0.025 in. between the electrodes were used. A device of this type might be modified to measure the small scale fluctuations in the ocean.

PRESSURE SENSING DEVICES

The measurement of velocity can also be effected by measuring the associated pressure which varies as the square of the flow velocity. The devices which measure pressure are usually of two general types: mechanical devices which use the displacement of a wheel or plate to measure the pressure, and pressure sensitive crystals which generate e.m.f. when a pressure is applied to them.

The mechanical devices use either a plate which is mounted at right angles to the flow or a propeller whose axis is parallel to the flow. In some meters the pressure is registered by means of a plate hanging under gravity; however, any variation in tilt of the meter will introduce errors into the readings. Plates controlled by spiral springs will obey the square law relation between pressure and velocity so that the readings in the low velocity range will be compressed into much smaller plate movements than those for the higher velocities. A device which has a relatively linear response to velocity changes is described by Doodson (1940).

The Doodson current meter uses a propeller which is restrained by a spring. The spring is connected to a lever arm which is rigidly attached to the propeller shaft. As the propeller rotates and the angle between the spring and lever arm changes there are two effects: the tension in the spring increases, and there is an increase in the moment of the tension. These effects combine to make the angular rotation of the propeller a linear relation of flow velocity. By limiting the maximum rotation of the propeler to 60° the inertial effects are made small so that the meter will have a reasonable response to turbulent fluctuations. Bowden and Fairbairn (1952a, 1952b) describe the use of Doodson meters to measure turbulent velocities in the River Mersey.

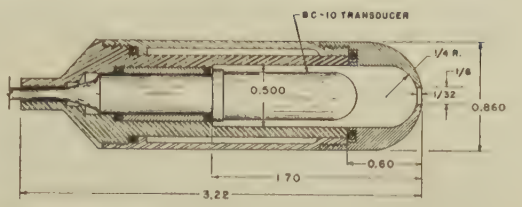

FIG. 1. Section view of pressure-transducer probe.

Meters of the Doodson type will have much longer response times than a device which uses a pressure sensitive crystal as a detector. Effort has been made at the Pacific Naval Laboratory to obtain a detector of small dimensions and with a short time response for turbulence measurements in our water tunnel. The detector being used at present is shown in Figure 1 and consists of a barium titanate BC-10 pressure transducer (Atlantic Research Co., Alexandria, Virginia), with suitable shielding so that it is sensitive to velocity fluctuations in the direction of the mean flow. The frequency response of this gauge is from 1–2 cycles per second at the low end and can go as high as several kilocycles. The limit to the response at the higher frequencies is the ⅛ inch opening at the front of the shielding which limits the resolution to turbulent scales of about that dimension. The gauge was used in conjunction with the hot-wire equipment at sea, and from the preliminary results it appears that the pressure sensitive

gauge will measure the small scale turbulent eddies much better than the hot-wire.

NEUTRALLY-BUOYANT FLOATS

The larger scale current fluctuations in the ocean can be followed by means of neutrally-buoyant floats described by Swallow (1955, 1957a, 1957b). The technique described by Stommel (1955) of using neutrally-buoyant floats which drop bombs at predetermined times so that the floats can be tracked by SOFAR would facilitate the measurement of currents over large areas.

HOT-WIRE FLOWMETER

The hot-wire circuitry as developed at the Pacific Naval Laboratory is shown in Figure 2. The system is a constant-temperature hot-wire which is heated by an alternating current. As the water flows by the hot-wire some of the heat is transferred from the wire to the water and the greater the water velocity the greater the amount of heat transferred. When the temperature of the hot-wire changes due to the changing turbulent velocities, the bridge becomes out of balance and an "error voltage" signal is fed to the negative feedback amplifier which adjusts the heating current in the hot-wire to compensate for the induced temperature change and maintains the hot-wire as close as possible to a constant temperature. This "error voltage" is also fed back through amplifiers to pen recorders and a two-channel tape recorder. In order to record the very low frequencies, the tape recorder which normally runs at 15 in./sec was run at 1/5000, 1/1000, or 1/150 of its normal speed by means of a special drive. Recently the signal from the hot-wire has been tape recorded using a frequency modulation system and the different frequency ranges obtained by re-recording at different speeds in the laboratory. This system has the big advantage that the full range of frequencies can be recorded at once. The final tape records are played back at normal speed and analyzed on a frequency spectrum analyzer.

The alternating heating current was originally chosen because the matching of the low resistance, high current characteristics of the hot-wire to the high resistance, low current characteristics of the hot-wire bridge by means of a transformer could be more easily done for A.C. than for D.C. It has been shown by later work in this laboratory and by Hubbard (1954) and Stevens, Borden and Strausser (1956) that the use of an alternating heating current overcomes instabilities due to bubble formation on the wire and polarization of the water.

The hot-wire, which has to be strong mechanically and resistant to sea water corrosion, was originally a teflon-coated copper wire and in the latest equipment is either a platinum or platinum-coated tungsten wire of about 1 ohm resistance. Tungsten which has better characteristics for hot-wire use could not be used due to the difficulty of attaching it to the hot-wire probe. The length of the teflon-coated wire was about 2 inches and this length was reduced to one inch for the platinum wires. Originally the wires were mounted at right angles to the flow but it was found that during plankton blooms the wire very quickly became coated and the response of the wire dropped off drastically. By mounting the wires at 45° to the flow the plankton were shed and the usefulness of the probe was extended over longer periods of time (Fig. 3).

The hot-wires are heated to about 20°C above the ambient water temperature, and by comparing hot-wire records and cold-thermistor records it was found that temperature fluctuations of the order of $\frac{1}{10}$°C were not recorded by the hot-wire; however, when the temperature fluctuations were of the order of 1°C the turbulent microstructure was masked by the temperature microstructure. If temperature microstructures with a variation of the order of 1°C were normally encountered the hot-wire probe would have to be modified. Hubbard (1954) does this by putting one of the arms of the hot-wire bridge near the hot-wire so that it balances the change in resistance in the hot-wire due to the temperature fluctuations in the water.

From work done in the sea it has been determined that scale sizes larger than one to two inches can be measured with reason-

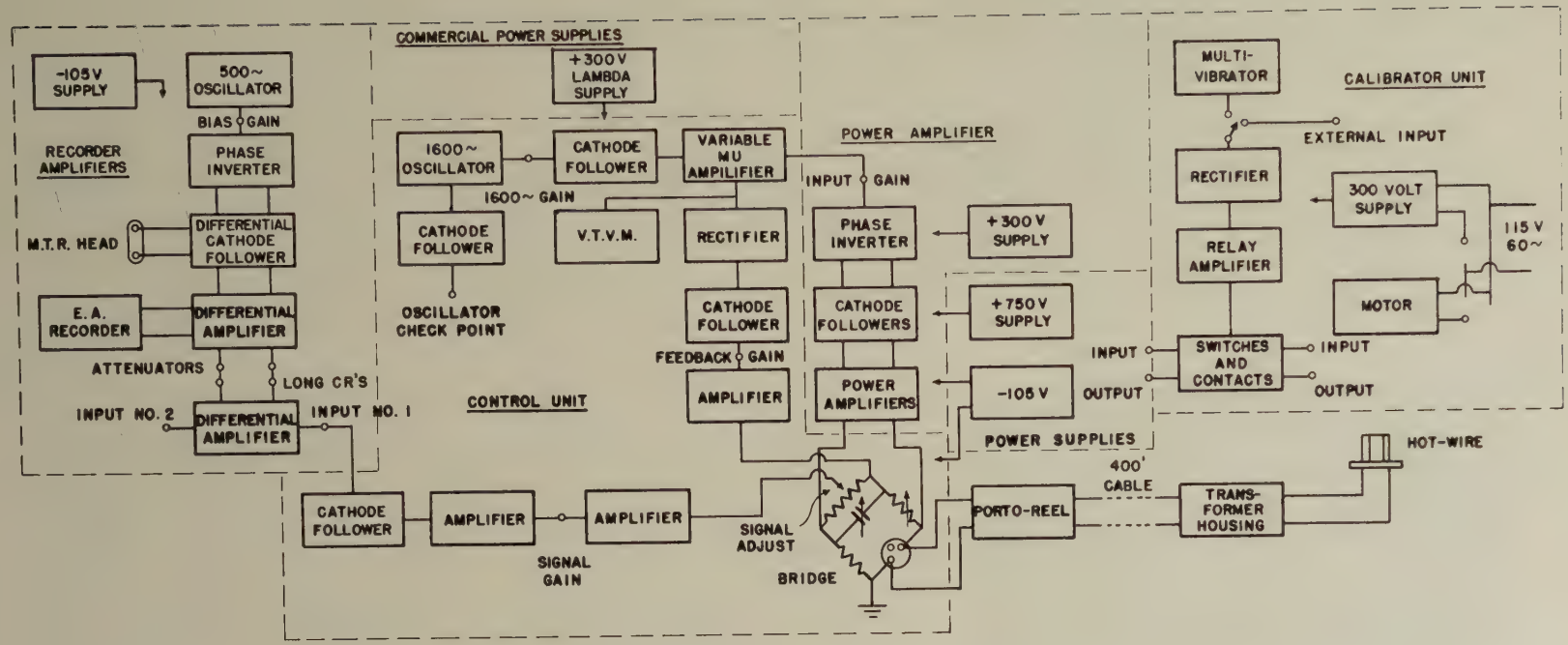

FIG. 2. Block diagram of hot-wire circuitry.

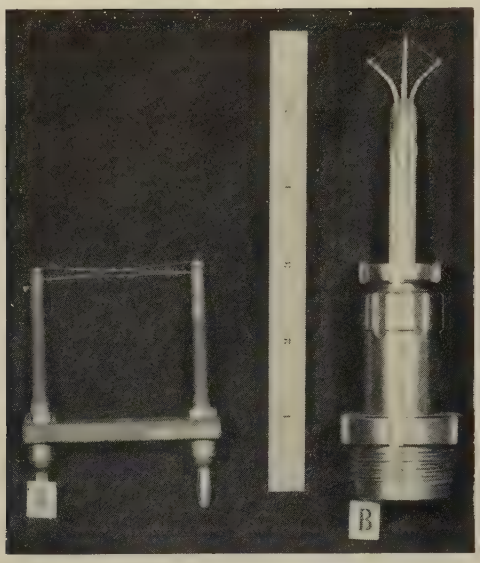

FIG. 3. Hot-wire probes: *A*. Teflon-coated copper wire probe; *B*. Platinum V-probe.

FIG. 4. Underwater portion of hot-wire equipment.

able accuracy with a hot-wire, and that smaller scales can more easily be measured with a pressure transducer. As a result the length of the hot-wire need not be shorter than about 1 inch. A platinum or platinum-coated tungsten wire of this length, having a resistance of 1 ohm, has good mechanical strength and is easily attached to the wire supports. Another good feature of this wire is that the equivalent sea-path resistance is much higher than 1 ohm and therefore changes in resistance in the water will not introduce appreciable errors into the hot-wire readings.

If the hot-wire is towed through the water at 3 knots a scale size of 1 inch requires that the hot-wire have a frequency response somewhat higher than 60 cycles per second. In order to ensure that the hot-wire will have this response the frequency of the heating current must be at least 10 times as high or a minimum of 600 cycles per second. The existing hot-wire equipment uses a heating current having a frequency of 1500 cycles per second.

The underwater portion of the hot-wire gear, shown in Figure 4, is hung over the side of a ship and towed through the water at about three knots. The hot-wire probes are suspended below the spar so that they are out of the wakes of the towing cable and spar. The weight hung below the spar is used to keep the apparatus down in the water, and the high drag tail keeps the probe pointing into the mean flow. The transformer can be seen mounted on the spar just behind the hot-wire support spar. The gear has usually been towed at a depth of between 6 to 10 fathoms, this depth being limited by the depth of water in which we have been doing turbulent microstructure measurements.

SOME TURBULENCE MEASUREMENTS WITH HOT-WIRES

To date no attempt has been made to make absolute measurements of the intensity of the turbulence. Most of the work has been to obtain turbulent spectra and to determine their variations due to turbulent decay or to generation of new turbulence by obstructions in the flow. An attempt was made to measure the decay of turbulence from Ripple Rock in Seymour Narrows on the eastern side of Vancouver Island by anchoring at three stations in Discovery Passage below Ripple Rock. It was found that the turbulence decay of the

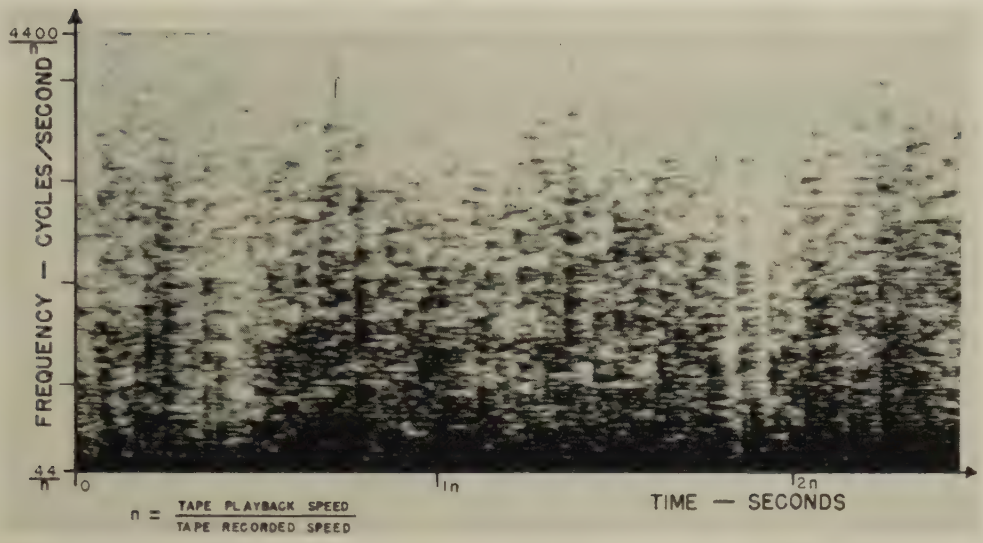

FIG. 5. Typical vibragram of the turbulence signal.

wake of Ripple Rock was masked by the generation of turbulence on the bottom and sides of Discovery Passage so that no variations in the turbulence spectra could be observed. Attempts have also been made to obtain records of the turbulence generated by Constance Bank, a bank in the Victoria Harbour approaches which rises to within 8 fathoms of the surface from much deeper water. Although there have been indications of the generation of new turbulence by the bank, the very high background turbulence which exists in the Strait of Juan de Fuca makes positive identification very difficult. Use now being made of the pressure transducer to measure the smaller turbulent scales should give us better results.

The tape-recorded turbulence signals are analyzed on a frequency spectrum analyzer called a Vibralyzer (Kay Electric Co., Pine Brook N. J.). A portion of the tape record is re-recorded on the circumference of a magnetic disk. The signal on the disk is scanned by a band-pass filter which is shifted each revolution of the disk, and the output is then recorded on dry facsimile paper. The first paper record, called a Vibragram (Fig. 5), plots the signal frequency vs time, with the darkness of the trace indicating the magnitude of the energy level of the signal. Because the amplitude or darkness of the trace is not too well defined, due to the limitations of the paper, this record is used to determine the general variations in the turbulence signal and to select points on the record at which time averages of the signal are to be taken. The second record, called a Section, portrays the amplitude vs frequency of the signal at the preselected points. Two types of portrayals can be made, the logarithm of the signal amplitude or a linear representation of the signal amplitude. Both have uniform scales which cover 35 db. for the logarithmic plot and a range of 10 to 1 for the linear plot, the scales being relative to 1 millivolt. For most of the work it was found that the logarithmic representation was more useful because it corresponds to the logarithm of the square root of the energy content of the different scales of the turbulence. The logarithmic record is referred to as the turbulence spectrum.

The spectra in Figure 6 are 1.25 minute averages of the turbulence signal taken at about half-hour intervals during one of the operations near Constance Bank. These records are typical of those obtained in the Strait of Juan de Fuca for the turbulence scales from about 10 to 600 feet. The short time averages show that there are large vari-

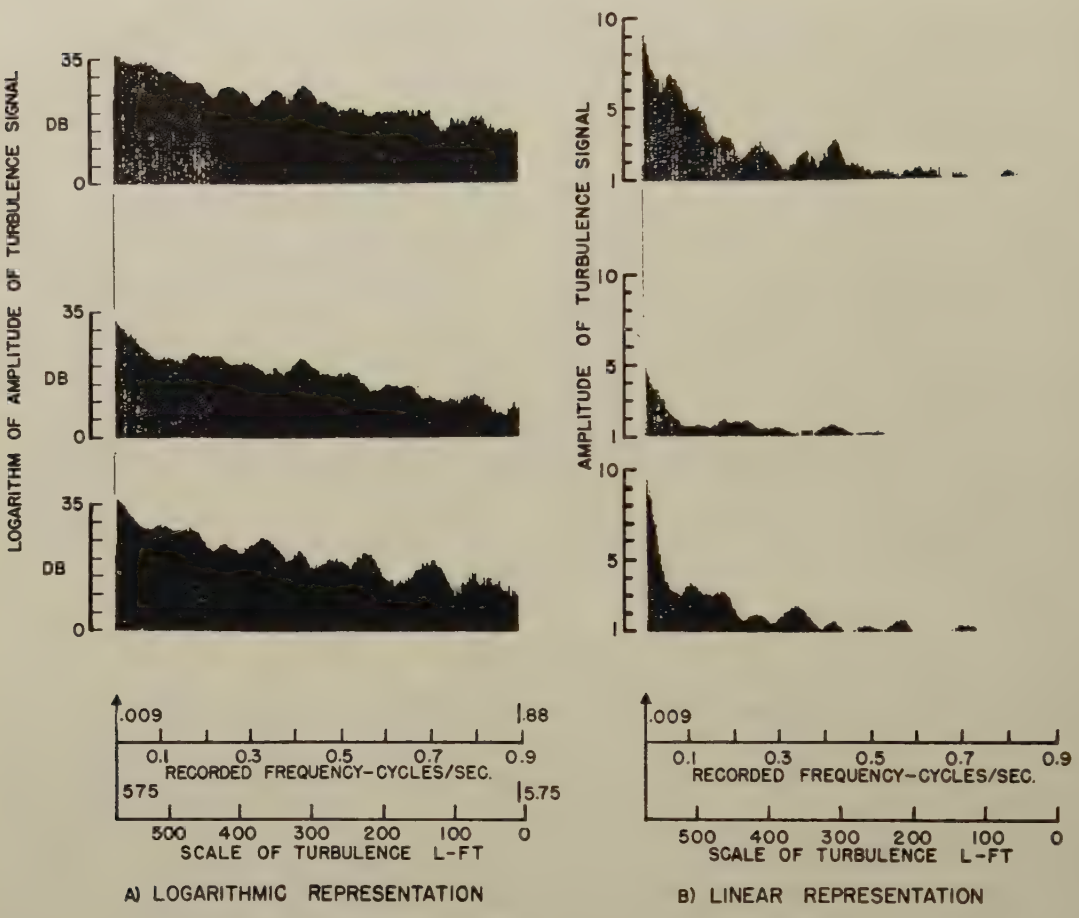

FIG. 6. Spectrum of turbulence near Constance Bank.

ations of energy content of the different turbulence scales with time; however, when long time averages are taken the spectrum becomes a smooth curve with the energy decreasing from the large scales to the smaller scales. Although the total energy content of the turbulence changes at different times over a tidal cycle, the general shape of the spectrum for these scales remains essentially the same. The changes in the spectrum take place in the turbulence scale sizes from about 15 feet down to fractions of inches.

An investigation of the change in the turbulent spectra over a tidal cycle in the Strait of Juan de Fuca near Victoria showed that there were smaller scale eddies during the flood and ebb tide periods, and that during the slack-water periods the decay in the turbulence reduced the amplitude of the small scale eddies. As the slack-water periods were of short duration no marked decay of the turbulence took place.

The clearest indication of the change in turbulent spectra due to an obstruction in the flow was obtained near Race Rocks in the Victoria Harbour area. Race Rocks is a series of rocky islands which rise out of 40-fathom water. As the tide sweeps past these islands at up to 4 to 6 knots, a wake is generated behind each island, and from the largest island there appeared to be an eddy shed which was similar to a Kármán Vortex Street. At the surface these large eddies appeared quite distinct from the rest of the flow near Race Rocks and gradually decayed downstream, eventually becoming indistinguishable from the general turbu-

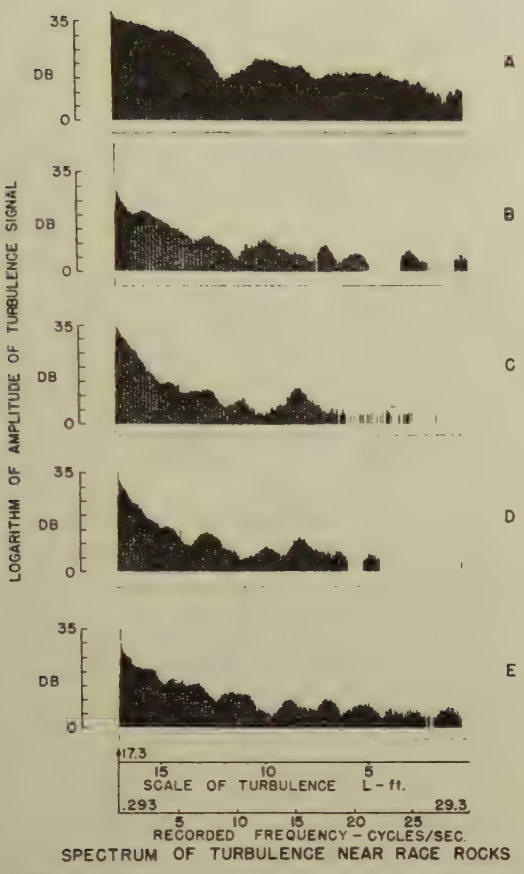

FIG. 7. Spectrum of turbulence in an eddy near Race Rocks.

lence. By towing a hot-wire through one of these eddies near Race Rocks the spectra in Figure 7 were obtained.

Near the center of the eddy the water should be rotating as a solid body but toward the outside of the eddy, interaction with the surrounding water would break down the main motion so that smaller eddies appear. When towing a hot-wire through the eddy the spectra should show high frequencies (small scale fluctuations) at the edge of the eddy which are reduced in amplitude as the center of the eddy is approached. The spectra in Figure 7 are 2¼-second averages taken at equal time intervals from one side of the eddy to the other and show that this is what was being observed. The spectra *A* and *E* are near the edge of the eddy and exhibit higher frequencies than *C* which was near the center of the eddy. Spectra *B* and *D* are from positions intermediate between the edge and center of the eddy. No statistical significance can be attached to the peaks in the region from scale sizes of 17.3 feet to about 7 feet as they will tend to average out when longer time averages are taken. The scale sizes from 7 feet down have statistical significance in the short time average shown, and indicate that the further out from the center of the eddy the smaller the turbulence scale that is being generated, and that the energy content of these small scales increases towards the outside of the eddy. As the hot-wires were not calibrated the magnitude of the signal could not be used to obtain absolute measurements but gave the variation in the energy content of the different scale sizes with time.

Although most of the work which has been done at the Pacific Naval Laboratory has been carried out in the Strait of Juan de Fuca there is no reason to believe that hot-wire turbulence measurements cannot be done in the open ocean. The problem of the very small scales would be eliminated unless the turbulence near the bottom were of interest, and the problem of plankton would be reduced so that the hot-wire could be very useful for turbulence measurements in the open ocean provided the difficulties introduced by ship motion can be overcome.

Instruments are now available or shortly will be available which will measure turbulent velocities from scale sizes of the order of several millimeters up to scales which depend on tidal changes. Therefore the time is ripe for a widespread study of ocean turbulence to obtain information required by all those engaged in doing oceanographic research.

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A Portable Core Sampler for Lake Deposits

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ABSTRACT

A pneumatically operated core sampler is described which is easily portable and may be used by two men from a rowing boat. The apparatus takes an undisturbed sediment core 6 m long and is substantially independent of water depth up to a limit of some 250 m. The hydrostatic pressure operating on a cylindrical anchor chamber embedded in the sediment is used to hold the apparatus in contact with the bottom while the coring tube is driven downwards by compressed air. On completion of the coring operation, the anchor chamber is automatically filled with air, the coring tube is extracted from the sediment, and the apparatus brought to the water surface by the buoyancy lift. The use of heavy weights and the associated lifting tackle is therefore avoided.

INTRODUCTION

The sediments at the bottom of a lake contain a record of the biological and chemical changes which have taken place in the system throughout the period of sedimentation. It is therefore important that samples of such sediments should be obtained for study without disturbing their sequence. A number of samplers which achieve this objective have been described, all of which suffer from some disadvantage when applied to limnological work. The Kullenberg and the Jenkin samplers (Kullenberg 1947, Jenkin *et al.*, 1941) both use heavy weights to drive the apparatus into the sediment, thus necessitating the use of heavy lifting tackle and relatively large vessels or floating platforms, neither of which is normally available on the majority of lakes. The field of limnological operation of these instruments is therefore limited. The difficulties of transportation and handling inherent in the Kullenberg and Jenkin samplers were overcome by Livingstone (1955) who described a piston sampler which is similar in principle to the Kullenberg sampler, but is pushed into the sediment by hand by means of a long jointed rod. While the apparatus obtains very satisfactory cores, great difficulty is found in operating in water depths greater than 20 meters because of the flexibility of the rod used to push the sampler into the sediment even when the rod is stiffened by a casing pipe. This depth limitation is serious when samples are to be taken from deep lakes, since it is well known that the shallow water sediments of such lakes are not typical and may differ widely from the sediments in the deep water of the same basin. It was therefore desirable to devise an apparatus which, while being readily portable, could be used in any depth of water likely to be encountered in the lakes of the English Lake District (up to 80 metres). This objective was achieved by means of the apparatus here described.

The author wishes to acknowledge the enthusiastic work of Mr. W. C. Findley and Mr. J. B. Anderson who built the apparatus in the workshop, the generosity of Mr. A. B. I. Dick of Messrs Talbot Stead Ltd., for the gift of the stainless steel tube, and the helpful criticism of the manuscript by Mr. H. C. Gilson.

GENERAL DESCRIPTION OF APPARATUS AND MODE OF OPERATION

An outline of the apparatus is shown in Figure 1. *A* is a 20-ft length of stainless steel tubing 3 in. external diameter. The lower end of this tube is fitted with a flange which is bolted onto the upper surface of the drum *G*. The latter consists of a cylinder of sheet steel closed at the upper end by a steel plate. This cylinder is 18 in. in diameter and 4 ft high and open at the lower end, and is subsequently referred to as the anchor chamber.

Inside the stainless steel tube is the coring

tube B which is a 20-ft length of "Duralumin" scaffold tubing. This tube is inserted at the upper end into the piston C which closely fits the bore of the tube A. In the lower end of the coring tube B is a piston F. This piston is attached by means of the narrow tube D to the plug L which closes the upper end of the stainless steel tube A, so that the piston is unable to move downwards in relation to A. The narrow tube D passes through a sliding pressure seal in the centre of piston C so that this piston and the coring tube may move downwards, the coring tube passing through a clearance hole in the centre of the upper plate of the anchor chamber.

In operation an air pressure hose is attached to the tube E which passes through the plug L, and a plastic hose P is connected to the tube H which passes into the anchor chamber. The apparatus is lowered by means of a rope fastened to a chain bridle at M until the lower part of G comes into contact with the sediment. While a small constant tension is kept on the rope to ensure that the instrument remains vertical, water is pumped from the anchor chamber through the hose P. As water is withdrawn, the hydrostatic pressure pushes the anchor chamber into the sediment until when mud emerges from the hose the upper plate of G is level with the sediment surface. The upper end of the hose P is now closed, and the anchor chamber now embedded in the sediment is capable of resisting a considerable upward force because of the hydrostatic pressure which comes into play as soon as any such force is applied. Compressed air is now admitted through E. The pressure in the space Q drives the piston and coring tube downwards until the lower end of the piston C is stopped by the flange K (Fig. 3) on the upper plate of G. When the piston C passes the point R, the compressed air behind C passes through the hose I into G. The entry of air under pressure lifts the anchor chamber out of the sediment with considerable force. (Since the area of the upper plate of G is 250 in.^{2} an excess of 10 lbs/in.^{2} over the external pressure exerts a lifting force of about 1 ton.) This initial lift also extracts the coring tube, since C is resting on the upper plate of G. When the anchor chamber is full of air and it has risen almost clear of the sediment surface, the buoyancy lift of G completes the extraction and lifts the apparatus to the water surface. The buoyancy of the anchor chamber when full of air is equal to an uplift of some 450 lbs which brings the apparatus to the surface with considerable violence. This violence is moderated by the release valve at J (described later) which allows most of the air to escape during the ascent when the core tube has been completely extracted. The apparatus is then taken ashore and the core extracted hydraulically into suitable containers. The manner of extraction of the core is described in the section on handling the apparatus.

CONSTRUCTIONAL DETAILS

The tube A in Figure 1 is of stainless steel 20 ft long, 3 in. external diameter, wall thickness $\frac{1}{16}$ in. It is fitted with a welded flange at the lower end which is 6 in. in diameter, $\frac{3}{8}$ in. thick, and drilled with 4 equally spaced clearance holes to take the $\frac{3}{8}$ in. bolts (G_1 in Fig. 3). The inside of the tube is polished. The upper end of the tube A is closed by a "pickle-bottle" seal L in Figure 1. Details of this sealing arrangement are shown in Figure 2. L_1 and L_6 in Figure 2 are brass discs which are a sliding fit into the bore of the tube A and respectively $\frac{7}{16}$ in. and $\frac{3}{4}$ in. thick. Both discs are drilled centrally with clearance holes for the brass tube D ($\frac{3}{8}$ in. external diameter.) L_2 is a rubber disc of the same diameter $\frac{1}{4}$ in. thick and drilled in the center to fit the tube D. Two diametrically placed $\frac{3}{8}$ in. bolts (one of which is shown dotted at L_4) pass through clearance holes in L_6 and L_2 into blind tapped holes in L_1. The tube L_5 which is threaded to take a standard $\frac{1}{4}$ in. gas nipple at L_8 is brazed into L_6, and the lower end of the tube is turned down to pass through a clearance hole in L_1 and L_2. This assemblage is anchored to the stainless steel tube by 4 equally spaced radial OBA screws (L_3) which pass through the wall of tube A into threaded holes in L_6. Two of these screws serve to attach by means of two small steel plates

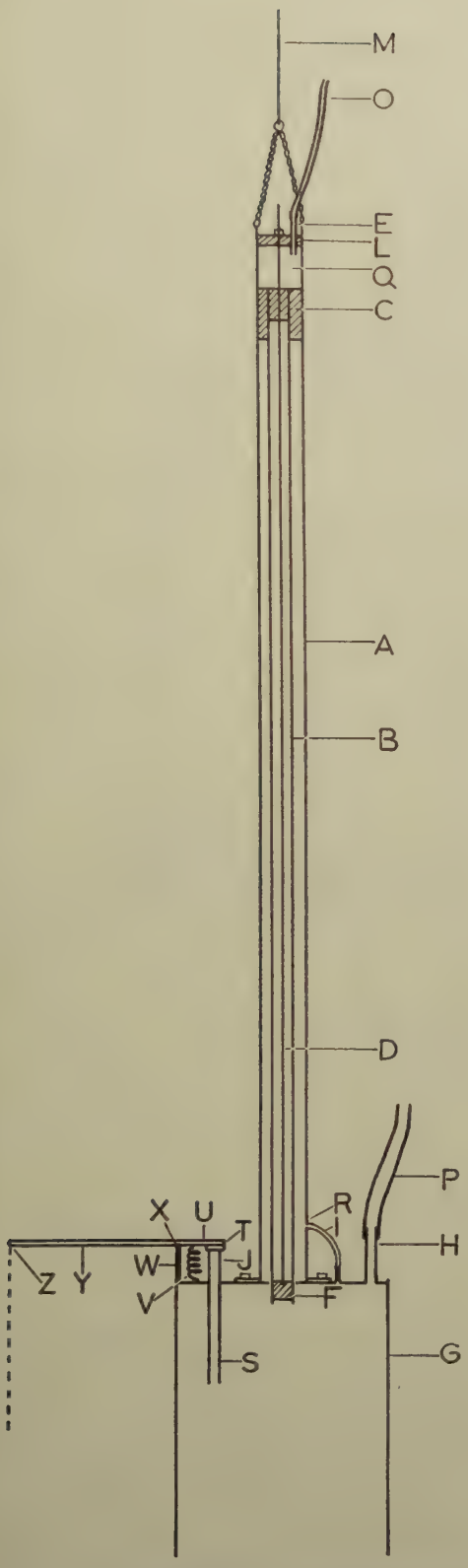

FIG. 1. Diagrammatic cross section of the complete apparatus, not to scale. Letters referred to in the text.

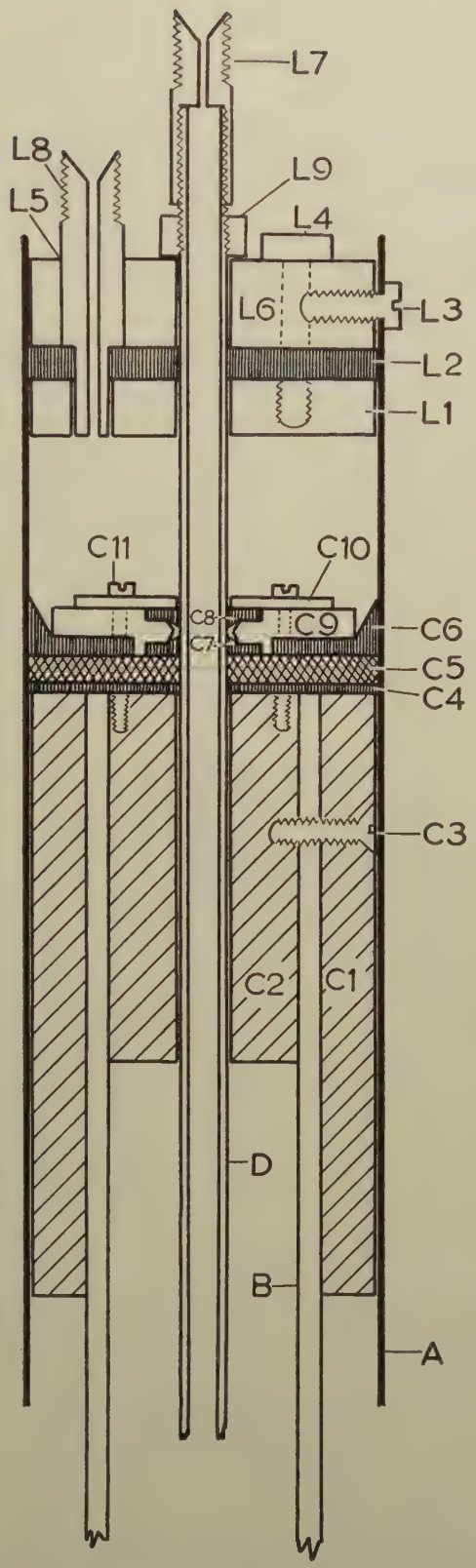

FIG. 2. Details of the sealing components of the upper end of the apparatus and of the driving piston. Letters referred to in the text.

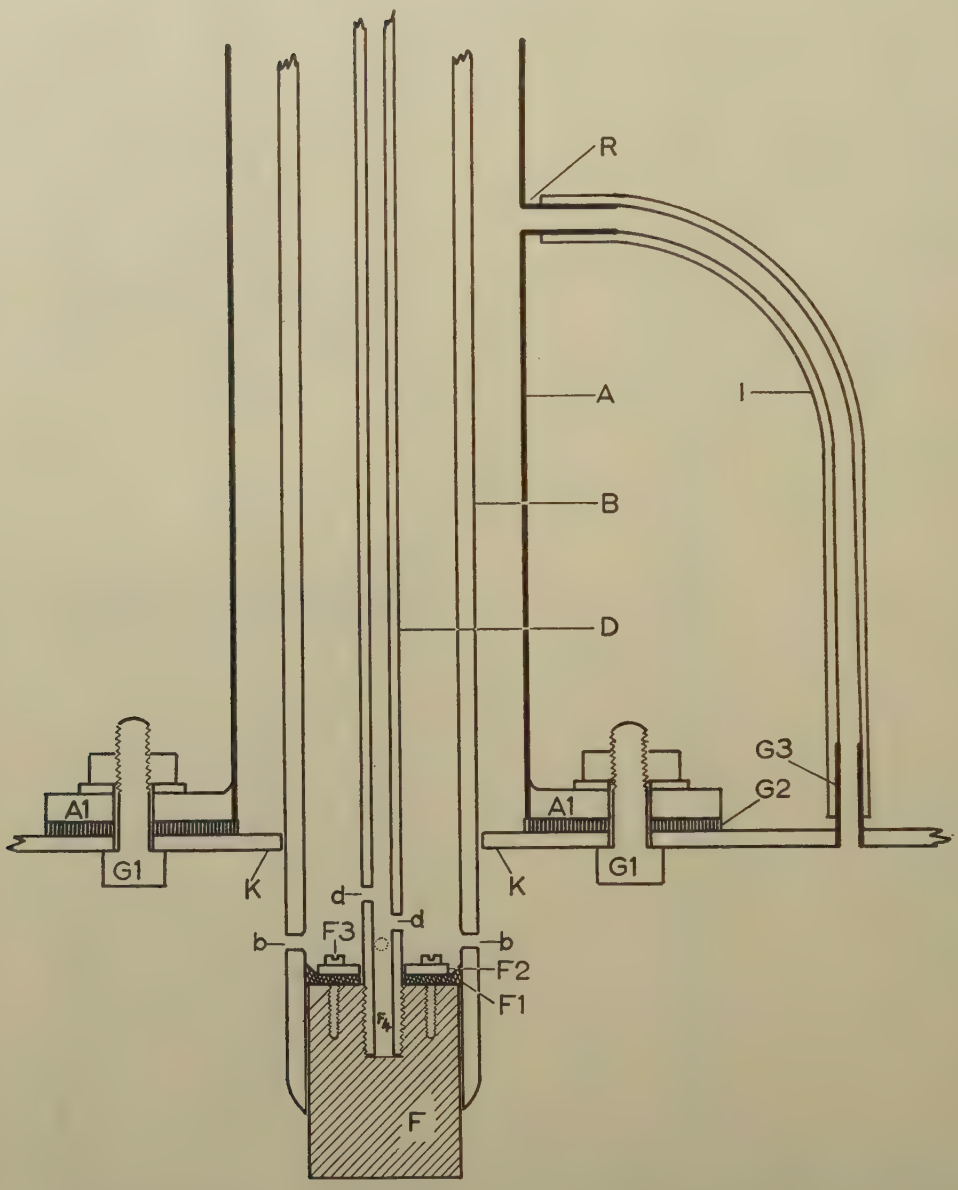

FIG. 3. Detail of the lower end of the apparatus before a core is taken. Letters referred to in the text.

⅛ in. thick (not shown) the chain to which the lowering rope is fastened to the apparatus. When the assembly has been fixed into the tube A by the screws L_3, tightening the bolts L_4 compresses the rubber disc and produces an effective pressure seal. The narrow tube D is 20 ft 4 in. long, of ⅜ in. external diameter brass with walls $\frac{1}{16}$ in. thick. This was built from shorter lengths with brazed spigot joints carefully smoothed on the outer surface. The joints should be strong since a substantial load in tension must be carried by D during hydraulic extraction of the core as is explained later. D is threaded at the top for the 1½ in. which protrude through the plug L, and is prevented from moving downwards in relation to L by the nut L_9. The upper end of D is fitted with an adaptor L_7 of hexagon brass screwed to take a standard ¼ in. gas

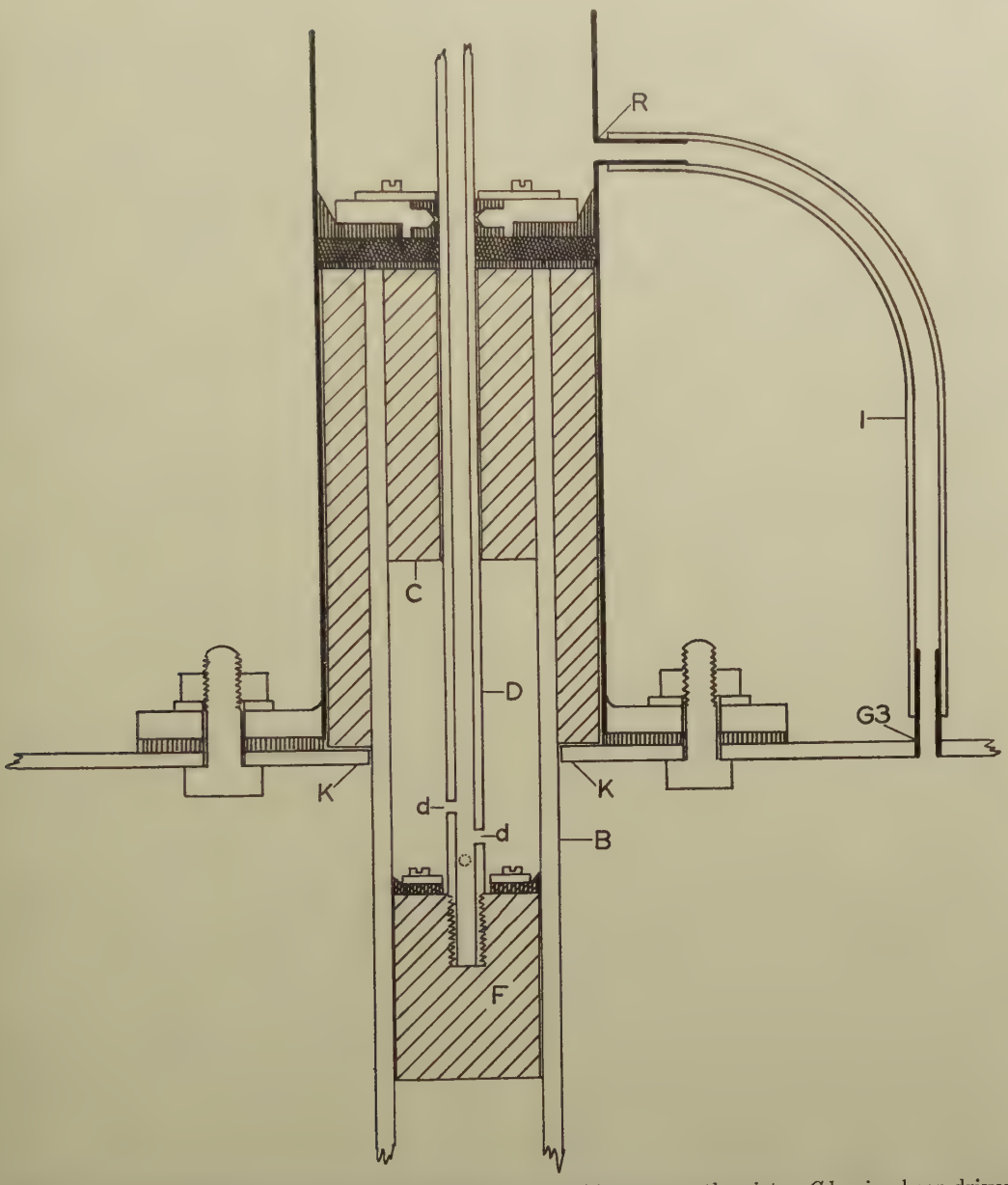

FIG. 4. Detail of the lower end of the apparatus after taking a core, the piston C having been driven down the length of the tube A in Figure 1. Letters referred to in the text.

nipple. D passes axially down the length of the apparatus to the piston F which is screwed onto its threaded lower end. D is pierced at the lower end just above F by three $\frac{1}{8}$ in. holes (d in Fig. 4) spaced as shown to preserve the strength of D. The function of these holes is explained below.

The piston C in Figure 1 is shown in detail in Figure 2. C_1 is a cylinder of brass which is a tight fit onto the outside of the upper end of the "Duralumin" coring tube B. This cylinder is a sliding fit into the bore of tube A and is 5 in. long. The cylindrical brass plug C_2 is a tight fit into the bore of B and is 3 in. long. C_2 is drilled axially with a clearance hole for the tube D.

C_1 and C_2 are pushed into place on the upper end of B until the ends of all three are flush. This assembly is then locked in position by the insertion of 3 equally spaced OBA countersunk screws which pass radially through C_1 into C_2. One of these screws is shown at C_3 in Figure 2.

The sealing components of the piston C are also shown in Figure 2. C_4 is a disc of rubber $\frac{1}{8}$ in. thick, its diameter equal to the bore of A ($2\frac{7}{8}$ in.) with a central hole fitting the outside diameter of D. C_5 is a similar disc of leather $\frac{1}{4}$ in. thick. C_6 is a neoprene cup washer $2\frac{7}{8}$ in. in diameter, sealing the bore of A from pressure from above. C_7 and C_8 are two small neoprene oil seals arranged back to back so as to produce a sliding seal on D which is effective against pressure applied either from above or below. The brass washer C_9 is $\frac{1}{4}$ in. thick, $2\frac{3}{8}$ in. in diameter, drilled in the centre to take D and shaped as shown in Figure 2 to accommodate and support the neoprene seals C_6, C_7, and C_8. C_{10} is a plain brass washer $2\frac{1}{4}$ in. in diameter drilled centrally to clear D. These components are assembled as shown in Figure 2 and held in position by two 2 BA screws C_{11} which pass through the assembly into tapped holes in C_2. With the piston assembly in place inside A, the screws C_{11} are tightened to compress the discs C_4 and C_5 against the bore of A, until the piston is sufficiently tight in the bore to prevent the coring tube sliding down under gravity when the apparatus is suspended vertically. It should be just comfortably possible to push the piston down the bore of A by hand.

The coring tube B is a 20-ft length of 2 in. external diameter, $\frac{3}{16}$ in. wall "Duralumin" scaffold tubing. This tube was smoothed internally before assembly, in order to ensure the sealing of the piston F (Figs. 1 and 3). The tube is held at the upper end by the piston C, which lies initially in contact with the upper plug L, and passes co-axially down the length of the tube A to protrude approximately 2 in. beyond the flanged lower end of A, passing through a central clearance hole in the upper surface of the anchor chamber G (Fig. 1) when the apparatus is assembled.

The lower end of B is ground to a cutting edge (Fig. 3). The piston F (Fig. 3) is screwed to the lower end of tube D and fits the bore of B. F occupies the position shown in Figure 3 in relation to B when the apparatus is ready for operation. Approximately 12 equally spaced radial $\frac{1}{8}$ in. holes are drilled through the wall of B (b in Fig. 3) at a distance of $1\frac{1}{2}$ in. above the lower edge of B so that the holes lie above the piston F when the coring tube is fully home in A. These holes allow water to enter the bore of B when the apparatus is lowered into the water, and prevent the increasing hydrostatic pressure from pushing F up the bore of B, which would be likely to damage the tube D (apart from other ill effects). The inside edges of these radial holes are carefully smoothed with carborundum paper to avoid damage to the cup leather of piston F when the coring tube slides over F during operation.

The piston F is made from a rod of "Duralumin" which is a sliding fit in the bore of B. It is drilled and tapped centrally with a blind hole on the upper surface to take the screwed lower end of D. The leather cup washer F_1 is a tight fit against the inside wall of B and is held in place by the washer F_2 and the two screws F_3 which pass through F_2 and F_1 into the duralumin rod.

The flanged lower end of A is bolted down to the upper surface of the anchor chamber by four equally spaced $\frac{3}{8}$ in. bolts G_1 (Fig. 3). The rubber gasket G_2 ensures an air-tight joint.

Six inches above the flange on A, at R in Figures 3 and 4, the wall of the stainless steel tube is drilled to take a brass tube 1 in. long of $\frac{1}{4}$ in. external diameter and $\frac{1}{8}$ in. internal diameter which is brazed into A. Any protrusion produced in the bore of A is carefully removed and smoothed to allow the piston C to pass freely. This short tube is connected by a length of flexible reinforced pressure hose I in Figure 3 to a similar short brass tube inserted and brazed through the upper surface of the chamber G at G_3 in Figures 3 and 4. The flexible hose is secured to the brass tubes at both ends by hose clips.

Figure 3 shows the relative positions of the components at the lower end of the

apparatus before a core is taken. Figure 4 shows this position after the coring tube has been driven into the sediment by the movement of the piston C down the length of the tube A after compressed air has been admitted through L_8 (Fig. 2). When the upper end of C passes the point R in Figure 4, compressed air is blown through I into the anchor chamber G. The air and water which occupied the bore of the coring tube B before the sample was taken are driven through the holes (d, d, d, in D) up the bore of D and out of the upper end at L_7 (Fig. 2). The bore of B below F now contains the sediment core. The lower surface of the piston C now rests on the upper plate of G at K (Fig. 4), so that as G rises from the sediment under the influence of the injected compressed air, the core tube is extracted with it.

The anchor chamber is constructed from .05 in. steel sheet rolled to form a cylinder and welded at the seam. The cylinder is 18 in. in diameter and 4 ft long, the upper end of which is closed by a circular steel plate $\frac{1}{8}$ in. thick, 18 in. diameter, welded into position. All the welded seams must be air-tight. The lower end of the chamber is left open, but the wall at the lower end is strengthened by welding on a hoop of $\frac{1}{8}$ in. thick steel 1 in. wide.

In the centre of the upper plate of G a clearance hole is cut to allow the coring tube to pass through it (see Figs. 3 and 4). The four $\frac{3}{8}$ in. bolts used to secure the flange of tube A to the top of the drum are passed through holes cut in the plate of G. The heads of these bolts are welded onto the underside of the plate. A steel tube (H in Fig. 1) 6 in. long, $\frac{3}{4}$ in. external diameter, $\frac{1}{8}$ in. wall, is inserted through the plate and welded into position. The hose P used in pumping water from the drum is connected to this tube and secured with a hose clip. A second steel tube S (Fig. 1) $1\frac{1}{4}$ in. external diameter, $\frac{1}{8}$ in. wall, is passed through the top plate of the chamber so that it protrudes 3 in. above and 9 in. below the top plate. The upper end of S which is machined square, is closed by a rubber disc T cemented into a steel cup which is welded to the steel bar U ($\frac{3}{4}$ in. $\times$ $\frac{3}{16}$ in. flat bar). The post W of $\frac{1}{2}$ in. square section bar welded to the edge of the anchor chamber plate, supports the arm U in a fork cut in the upper end of W, and U pivots about a $\frac{1}{4}$ in. bolt passing through the fork at X in such a way that the rubber disc may fit squarely on the upper end of S when U is pulled down by the powerful spring V. The outer end of U has a cylindrical piece of steel approx. 1 in. long welded on, the latter being threaded to receive the tubular steel extension arm Y 2 ft long, which may be detached for convenience in transport. In the field a light chain is shackled to the extension at Z. The chain is 15 ft long and is attached at the other end to an iron disc weight approximately 6 in. in diameter by 1 in. thick which weighs approximately 6 lbs. The spring V is chosen so that a downward pull is exerted on T equal to about 40 lbs. This would require the pressure within the anchor chamber to reach 50 lb/in.^{2} above hydrostatic pressure before the valve would open. Such a pressure is unlikely to be reached in practice since it would correspond to a lifting force on the chamber of about 5 tons which is probably much greater than the force required to extract the coring tube from the sediment.

When the apparatus is being lowered into the water, the weight is allowed to hang freely from the chain so that the valve is open until the weight reaches the bottom, when V pulls T into contact with the upper end of S. The valve remains closed until, after taking a core, the apparatus is rising clear of the sediment. It opens when the weight is lifted clear of the bottom, permitting air to escape through S until the water surface inside the anchor chamber has risen to the level of the lower end of S. The remaining air then brings the apparatus to the water surface reasonably gently.

ADDITIONAL EQUIPMENT

Sufficient air pressure hose is required to reach the bottom in the deepest lake in which it is desired to operate. The air hose is of the type used on gas welding equipment, $\frac{1}{2}$ in. external diameter with $\frac{3}{16}$ in. bore and with canvas reinforced rubber walls.

This hose has a working pressure of about 400 lbs/in.^{2}, but would probably stand a greater pressure before bursting. It is convenient to have the hose in sections of 30 m, the sections being coupled by standard gas nipple connections. One end of the hose is fitted with a nipple and nut for connection to the apparatus at L_8 (Fig. 2), and the other end has a suitable fitting for connection to a compressed air cylinder. A similar length of P.V.C. garden hose of ¾ in. bore is required, which is connected to the tube *H* in Figure 1 and secured by a hose clip. A rope of ½ in. diameter hemp or nylon is attached by means of a chain bridle to steel lugs fastened to the upper end of the apparatus by two of the radial screws holding the upper plug at L_3 in Figure 2.

Water is pumped from the anchor chamber through the P.V.C. hose. A convenient method of pumping the water out of the chamber is simply to inject air into the P.V.C. hose about 6 ft. above its connection with *G*. When air is injected into the water column in the hose, the density of this column is reduced in relation to the similar column outside the hose, and water is forced out of the anchor chamber and up the hose. Quite fast pumping rates can be achieved using this method which removes the necessity of carrying any pumping equipment. In practice air is injected into the P.V.C. hose through a stainless steel hypodermic needle. This should have a bore of not less than 1/16 in. and should be bent at right angles about ¼ in. from the point. The syringe end of the needle is securely fastened into the end of a rubber pressure hose which should be about 3/16 in. bore and strengthened by external braiding to stand a pressure at least equal to the hydrostatic pressure at the greatest operating depth. The point of the hypodermic needle is inserted into the P.V.C. hose 6 ft above the anchor chamber, so that the ¼ in. length of the needle which is bent at right angles lies within the P.V.C. hose. The rest of the needle is laid alongside the P.V.C. hose and taped into place with water-resisting polythene self-adhesive tape. The rubber hose from the needle is taped at intervals to the P.V.C. hose so that the two hoses may be handled as a unit. The upper end of the rubber hose is fitted with a suitable coupling for connection to the compressed air cylinder. It is convenient to take compressed air directly from the cylinder (normal commercial cylinders are used), without a reducing valve, since the ordinary reducing valve is not capable of giving a high enough pressure. The pressure and flow of air is controlled by the cylinder valve itself. A suitable pressure gauge reading up to some 400 lbs/in.^{2} is required, and care should be taken not to subject the gauge to the full cylinder pressure.

For hydraulic extraction of the core from the coring tube a hand operated water pump is used. The type of pump known as a "stirrup" pump which was issued to householders during World War II for fighting incendiary bombs is suitable. This pump is capable of producing a pressure of about 200 lbs/in.^{2} which is adequate. A short reinforced hose fitted with standard nipple for attachment to the upper end of the tube *D* at L_7 (Fig. 2) is connected to the pump.

OPERATION AND HANDLING

Given reasonable weather conditions, the apparatus can be handled by two men working from an ordinary rowing boat. It is seldom necessary to anchor the boat, since, when the drum has been pumped into the sediment, the apparatus is firmly attached to the bottom and serves as an effective anchor. It is convenient, however, to have a second boat in attendance which is used to tow the operating boat into position to avoid the inconvenience of operating oars or outboard motor in the same boat as the corer. The apparatus is carried in the boat lying fore and aft with the anchor chamber protruding over the stern. Before leaving the shore, the hoses and rope are attached to the apparatus, the air pressure hose at L_8 (Fig. 2) and the P.V.C. hose at *H* (Fig. 1). The hoses and rope are coiled into the boat. The upper end of the rubber hose which carries air to the hypodermic needle in the P.V.C. hose is connected to the compressed air cylinder. The boat is then moved to the site of operations. The extension arm of the release valve *Y* (Fig. 1) is screwed into

place, and the weight on the end of the chain is lowered into the water so that it is hanging freely. The apparatus is then slid over the stern and lowered by means of the rope while the hoses are payed out. As the apparatus is lowered into the water, the core tube is prevented from sliding downwards by the hydrostatic pressure acting on the leather seal C_5 (Fig. 2) apart from frictional forces. It is important that this seal is sound, otherwise with much use the movement of the piston C may become sufficiently easy to allow the corer to move downwards prematurely under gravity. The apparatus is not heavy to handle under water since enough air is trapped in the anchor chamber and the tube A to provide a considerable upthrust. When the anchor chamber reaches the sediment sufficient tension is maintained on the rope to keep the apparatus vertical to the mud surface. Air is now injected into the P.V.C. hose by applying a pressure from the cylinder to the air line connected to the hypodermic needle. The pressure should be maintained above the hydrostatic pressure. When air is injected into the P.V.C. hose, pumping commences and the upper end of the hose should be held over the side of the boat. As water is pumped out, the anchor chamber gradually sinks into the sediment and sufficient rope should be payed out to allow this while a sufficient tension is maintained to ensure that the apparatus is vertical. Pumping is continued until traces of the flocculent surface mud appear in the effluent from the P.V.C. hose. The plate of the chamber is now level with the mud surface, the chamber itself being entirely submerged in the mud. (This point was checked by divers of the East Lancashire Subaqua Club, for whose help the author is grateful.) The pumping time varies between 5 and 15 minutes depending on the water depth. The deeper the water the more efficient is the pump. The apparatus is now very firmly attached to the bottom, since any attempt to withdraw it is opposed by the hydrostatic pressure acting on the plate of the anchor chamber. The actual force required to lift the chamber out of the sediment has not been measured, but an upper limit can be calculated. Assuming (erroneously) that the mud is incapable of flow, if the operating depth is 50 metres, the pressure on the top plate when the chamber begins to be withdrawn is equal to 6 atmospheres, so that with an area of 250 in.^{2} the force required would be 22,500 lbs. This force would increase proportionally with depth. In practice, since the sediment is in fact capable of flow, the withdrawal force is likely to be much less than this calculated quantity but is nevertheless quite adequate to hold the apparatus in contact with the bottom while the core tube is driven into the sediment.

When pumping has been completed, the air hose to the injection needle is disconnected from the compressed air cylinder, and the upper end of the P.V.C. hose is closed either with a wide bore tap or by means of a plug held in place by a hose clip. The air pressure hose connected at L_8 to the apparatus is now connected to the compressed air cylinder, and air is admitted to maintain a pressure about 100 lb/in.^{2} above the hydrostatic pressure. This air pressure acting on the piston C (Fig. 1.) drives the core tube into the sediment. When the core tube has been driven in completely, C passes the point R (Fig. 1) and a sudden fall in pressure is observed as the compressed air in A is released into the anchor chamber. The core tube is driven in rapidly, less than 1 minute normally being required. The flow of air is continued in order to fill the chamber and extract it from the sediment. This operation may take several minutes, the time required naturally increasing with the depth of the water. If a steady tension is kept on the rope, the apparatus will be felt to be slowly rising as the chamber is ejected. When the anchor chamber is full of air, the buoyancy lift completes the withdrawal of the core tube, and the apparatus is felt to be rising rapidly clear of the bottom. The air supply should be shut off and the rope should be hauled in at this stage in order to have as little slack as possible. When the release valve opens as the weight hanging from the valve arm rises clear of the bottom, the rate of ascent is checked and it should be possible to keep up with the rising apparatus by

hauling in the rope. The apparatus usually surfaces almost horizontally, surrounded by air bubbles.

The apparatus should be prevented from sinking again (because most of the air in the chamber is lost at this stage) by again opening the compressed air cylinder and blowing air into the chamber. The rope should also be hauled in as quickly as possible. The apparatus should not be allowed to sink to any great depth after surfacing, since the hydrostatic pressure acting on the piston C tends to force the core tube back into A, which ejects part of the core from the lower end of the core tube. With a little practice the apparatus can be brought aboard the boat without much effort by judicious addition of air to the anchor chamber and manipulation of the rope. The corer is laid fore and aft in the boat, with the chamber about amidships and the core tube now extended lying on the stern. The hoses are taken aboard and the valve release weight hauled in. The boat is now taken ashore, and the apparatus laid on a suitable beach for extraction of the core.

To receive the core, 5′ 6″ lengths of trough are used. These may be made by splitting 2 in. internal diameter thin wall aluminium tubes lengthwise, or may be made from wooden planks joined at right angles to form a V-section trough. Four such lengths are required for each complete core. The end of the core tube is supported by placing a trough lengthwise under it, and supporting the trough on a wooden stand of a height slightly smaller than the radius of the anchor chamber. The air hose is disconnected from L_8 (Fig. 2), and the hose from the hand water pump is connected at L_7. The pump hose should be filled with water before connection to keep the volume of air in the system to a minimum. Water from a bucket is now pumped into the apparatus down the tube D (see Fig. 4). The water from D emerges through the holes d, d, d (Fig. 4) and into the space between pistons F and C. Since F is restrained from movement by D in tension, the pressure acting on C retracts the core tube into A, the core being simultaneously ejected as the core tube is retracted. This results in the core being left behind in the receiving trough as the core tube moves smoothly back into A. When the first trough is full the next trough is placed in position under the coring tube, and the supporting table is moved back toward the chamber by one trough's length. The troughs should be tightly held while the core tube is retracted so that they are not dragged along by the tube. Pumping is continued until the entire core has been collected in the four troughs and the core tube is again completely home in the tube A. This stage is reached when the pumped water is ejected from the radial holes in the end of the core tube (Fig. 3). The water pump is disconnected and the air pressure hose reconnected at L_8. The apparatus is now in the starting position and ready to take another core.

The cores lying in the troughs are wrapped in cellophane secured by adhesive tape for transport to the laboratory.

OPERATION IN SHALLOW WATER

In waters 25 m or less in depth, there is insufficient time for the air release valve to function before the apparatus reaches the surface. This results in a somewhat violent ascent which may damage the apparatus, boats, or operators. In shallow water it is therefore advisable to operate rather differently. The release valve is not used at all and the extension arm and weight are not connected. The apparatus is lowered to the bottom in the usual way but before pumping begins a float is secured to the rope at the water surface (a 5-gallon oil drum is suitable). The anchor chamber is now pumped out and the apparatus descends drawing the float under the water surface. The float now supports the apparatus vertically and the operators may retire to a safe distance before driving the corer in. After completion of the coring operation the apparatus rises to the surface and may leap out of the water with the anchor chamber clear of the surface. The apparatus is now approached and prevented from sinking as previously described.

CONSUMPTION OF COMPRESSED AIR

The amount of air consumed depends on the depth of water in which the apparatus is

operated. The deeper the water the fewer the cores which may be taken with a single air cylinder. In intermediate depths of some 50 m a standard 240 ft³ cylinder will take 3 or 4 cores. The cylinders could of course be replaced by a small portable air compressor capable of producing sufficient pressure for the operating depth required.

When working away from the laboratory, it is desirable to have a spare cylinder on hand in case of need.

TRANSPORT OF APPARATUS

For convenience in transport the anchor chamber is removed from the end of the stainless steel tube, the hose *I* (Fig. 3) being disconnected. The stainless steel tube with core tube inside can easily be transported on a small vehicle, lashed either alongside with suitable supports at the ends, or on the roof of the vehicle.

RESULTS

The cores obtained are cylindrical 1½ in. in diameter and 19 ft 6 in. (595 cm) long. There is no evidence of any distortion of the sediment strata, and the varves of the glacial clays lie quite flat in those localities where the sediments themselves have not been distorted by slumping on underwater slopes. The cores are large enough to allow relatively big samples to be taken for analysis from a narrow depth zone. Quite large pieces of organic debris, wood fragments, hazel nuts, and leaves are found in the cores which should enable sufficient carbon to be collected from a given depth to allow radiocarbon dates to be obtained.

The ease of transport and handling enables cores to be obtained from those lakes which are too remote for the Jenkin corer to be used and too deep for the Livingstone corer.

The length of the core in the present apparatus is limited to approximately 6 m by the length of the tube *B*. The apparatus could probably be made longer, but handling difficulties would perhaps become serious if the length were extended much above 9 m.

The depth of water in which the apparatus will operate is limited by the air pressures required to equal hydrostatic pressure. If one allows a practical limit of pressure at about 500 lb/in.² with the present hoses, this would limit the operating depth to about 280 m allowing for an operating pressure 100 lbs/in.² above the prevailing hydrostatic pressure. Such pressure limitation could be overcome by hydraulic operation of the apparatus rather than pneumatic operation, but the buoyancy lift of the drum would be lost and other arrangements would have to be made to lift the coring tube out of the sediment. It seems unlikely however that the present apparatus would be used in very great depths of water where a fairly large vessel would normally be available, permitting the Kullenberg corer to be used with advantage.

The advantages of the present apparatus lie in ease of transportation and speed of operation. It is possible in a day's expedition to visit the more remote lakes of this area and obtain several 6 m cores. When working on Windermere, with the apparatus at hand it is possible to obtain a deep water core almost as quickly as one would obtain a deep water sample.

SUMMARY

The sampling apparatus described has been used to obtain sediment cores 6 meters in length from relatively deep lakes. It may be handled by two men working from a rowing boat and is easily transported from lake to lake. The sampling tube is driven into the sediment and extracted pneumatically without the use of the heavy weights needed to operate the Kullenberg and the Jenkin samplers.

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Effects of an Arctic Environment on the Origin and Development of Freshwater Lakes[1]

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ABSTRACT

Thaw lakes beyond the glacial boundary in northern Alaska may be quiescent, with elliptical saucer-shaped basins, or they may be actively expanding, with deeply pocked basins. Glacial lakes of the usual types are found in the glaciated southern part of the region. The lakes freeze to a depth of almost 2 meters in winter and warm without stratifying to about 13°C in summer. Of the annual heat budget of some 28,000 cal/cm² only 6,000 cal is wind distributed. Total dissolved solids are known to range from 35 to 159 ppm, and the water is of a calcium bicarbonate type except where sea-spray influence is strong. The silica content is very low. A shore community is poorly-developed or absent, apparently because of ice-push, and the standing crop of benthos varies from an indetectable amount to 89.4 kg/ha. Remains of the midge *Dryadotanytarsus* are found throughout the sedimentary column of one lake, indicating that this genus, which is known only as a late-Pleistocene fossil, lives there today. The sediments of lakes receiving the products of the widespread processes of arctic weathering are very inorganic, with few and poorly-preserved microfossils. Computations based on a radiocarbon-dated pollen chronology suggest a net community productivity averaging less than 2 mg of organic matter/cm²/yr, and *Bosmina* and tendipedid productivities of less than 10/cm²/yr during the past 6,000 years. Further computations involving the data of other authors suggest that of the solar energy fixed by a temperate or arctic lake about one-quarter is preserved in the sediments, one-half is dissipated by the decomposing organisms and one-quarter is dissipated by all the other plants and animals. The arctic environment appears to influence lakes principally through physiographic processes affecting origin, sedimentation, and drainage.

INTRODUCTION

This paper is the result of two summers spent in the Brooks Range and Arctic Coastal Plain of northern Alaska. Observations made in the field and laboratory examination of the samples collected have provided more questions than answers, and the findings are presented as an introduction to rather than a complete monograph of the limnology of a very interesting region.

The area with which we are concerned lies north of the Arctic Circle. It is very cold and very dry. Weather stations are scarce, but at Point Barrow on the arctic coast, where records have been kept for over thirty years, the mean annual temperature is −12°C, and the mean annual precipitation 10.7 centimeters (U. S. Weather Bureau 1943). At Anaktuvuk Pass, in the Brooks Range, where a weather station has been maintained for two years, the mean annual temperature is −10.8°C, and the mean annual precipitation 34.6 centimeters (U. S. Weather Bureau 1956).

The dryness of the coastal plain and the foothills is so severe that they have never been glaciated. The Brooks Range was covered by ice at least four times during the Pleistocene, and it supports a few small

[1] Some of this material was embodied in a thesis presented by the senior author to the Zoology Department of Yale University in partial fulfillment of the requirements for the degree of Doctor of Philosophy. The field work and part of the laboratory work on which this paper is based were financed by Contract NONR/340(00) between Yale University and the Office of Naval Research of the United States Navy. The rest of the laboratory work was carried out at Cambridge and Dalhousie Universities during tenure of post-doctorate fellowships awarded by the National Research Council of Canada. Among the many people to whom the authors are deeply indebted for help, guidance, and encouragement are particularly Mrs. Bertha Livingstone, Professors E. S. Deevey, Jr., and G. E. Hutchinson of Yale University, and Dr. Ira L. Wiggins, former Director of the Arctic Research Laboratory. Dr. G. W. Whetstone of the Public Health Laboratory, Anchorage, Alaska, carried out most of the water analyses.

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cirque glaciers at the present time (Péwé *et al.* 1953).

The cold dry climate of the coastal plain is ideal for the accumulation of ground ice, and perennial freezing temperatures prevail to a depth of several hundred meters (Payne *et al.* 1951). Only the upper few decimeters of the land surface thaw out in summer, not only on the coastal plain but in the mountains and foothills as well.

The bedrock of the coastal plain is covered in most places to a depth of over thirty meters with the Pleistocene Gubic formation which consists largely of silt (Payne *et al.* 1951). So much ice has accumulated in the silt (Leffingwell 1915) that it constitutes a considerable fraction of the total volume of the formation.

The vegetation of northern Alaska varies from a subarctic mixture of boreal forest and tundra to an arctic tundra of herbs and prostrate shrubs. South of the Brooks Range divide most of the river valleys have stands of the *Picea-Populus-Betula* forest that covers the interior of Alaska (Hulten 1941). On the north side of the divide spruce seems to be almost absent, although there are local stands of *Populus* in a number of sheltered valleys (Leffingwell 1919, Spetzman 1951).

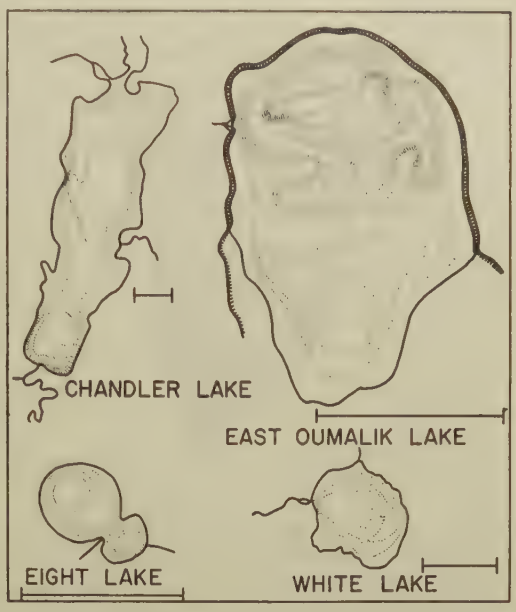

FIG. 1. Bathymetric maps of some representative Alaskan lakes. The length of the scale line represents 1000 meters in each case. The number of sounding runs for each map is: E. Oumalik L., 6; Chandler L., 3; White L., 2; Eight L., 1. The outline of Chandler L. is taken from the Alaska Reconnaissance Series Chandler Lake Sheet; of Eight L. from a field sketch; and of East Oumalik L. and White L. from vertical air photos. Contour interval: Eight L. and East Oumalik L., 1 m, Chandler L. 5 m, White L. 10 m.

METHODS

Core samples were taken from one or two pneumatic rubber dinghies with a Hiller sampler modified according to a suggestion by Erdtman (in Wodehouse 1935) to hold a removable metal liner, or else with a modified Kullenberg piston sampler (Livingstone 1955a). Microfossils were separated from their silty matrix by bromoform flotation according to the method of Frey (1951), and were counted at 100× magnification.

Relative chlorophyll contents were determined by measuring in a Beckman spectrophotometer at 6630 Å the absorption of the pigment extracted from one milliliter of wet lake mud by five milliliters of acetone.

ORIGIN AND MORPHOMETRY

Most of the lakes visited during this study owe their origin to the action of ice. The mountain lakes are of glacial origin. Some of them occupy kettles formed by the melting of buried glacier ice (see Fig. 12), while others lie in basins formed in part by glacial scour and in part by the damming action of moraines and fans.

The lakes on the coastal plain were formed in a rather different way. They are thaw lakes, resulting from the melting of large masses of ground ice (Hopkins 1949, Black and Barksdale 1949, Wallace 1948).

In the foothills between the Brooks Range and the coastal plain there are some lakes of other types, such as the numerous ox-bow ponds in the river valleys, but the only lake covered in the present study that was not clearly a thaw lake or a glacial lake or some combination of the two was Swallowtail Lake near Umiat, which appears to occupy a depression behind some material that has slumped off the hillside.

In the glaciated part of northern Alaska it is sometimes rather difficult to distinguish between thaw lakes and kettles. A lake

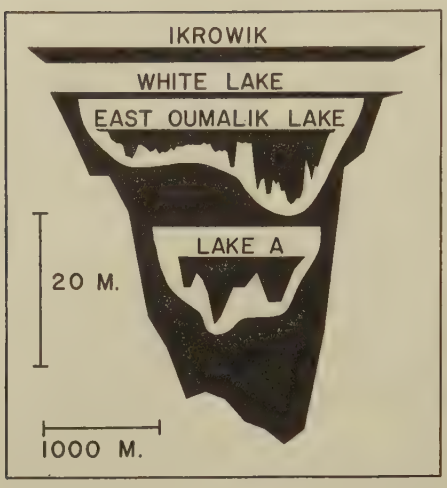

FIG. 2. Profiles of some representative Alaskan lakes. Ikrowik is a mature thaw lake, East Oumalik L. a youthful thaw lake, and the other two lakes occupy kettles.

that is primarily a kettle may be enlarged from time to time by the melting of ground ice in the surrounding material. Slumping and mudflow on the shores of a kettle may give it the superficial appearance of a thaw lake, and it is very difficult when examining an actively expanding lake in a body of till or outwash, to tell whether it is expanding at the expense of ground ice that has formed *in situ* or at the expense of buried remnants of glacier ice. Even though the outwash body may be very old the possibility that some glacier ice persists cannot be ruled out, because climatic conditions are extremely favorable for prolonged ice preservation.

Rough contour maps of a number of lakes appear in Figure 1, and representative profiles across a few thaw lakes and kettles are shown in Figure 2. The shape of the glacial lakes is not extraordinary, but that of the thaw lakes calls for some comment.

The profile of Ikrowik is characteristic of most of the mature oriented thaw lakes on the Arctic Coastal Plain in the vicinity of Point Barrow. Its outstanding property is remarkable uniformity. Once away from the shallows near shore one finds that the depth hardly varies by more than a decimeter over a distance of more than a kilometer.

Some aspects of the shape of these lakes have been discussed in an earlier paper (Livingstone 1954). It appears that they owe their great regularity, in profile as well as in plan view, to the system of circulation currents set up in them by the prevailing northeasterly winds. These currents take silt dislodged from the bank by the pounding waves and distribute it over the basin, filling in the hollows and producing a regular, shallow, saucer-shaped depression.

Lakes of the Ikrowik type lie in the low part of the coastal plain, where the relief and the elevation above sea level are only a few tens of meters. At the present time they appear to be draining about as fast as they are forming, and the processes of lake formation and drainage have been going on for some time, so that the land area of this part of the coastal plain seems to consist almost entirely of the drained basins of elliptical lakes. These drained basins are covered with a polygonal pattern consisting of low-centered polygons, which are young, and high-centered polygons, which are old. Black (1952), estimating the ages of some of the ice-wedges between these polygons by extrapolating present rates of growth, has come to the conclusion that some of them are about 3000 years old. The method is open to objection but it indicates an order of magnitude for the minimum time since the process of ice-wedge formation began around Point Barrow.

Away from the coast in the transition zone between the coastal plain and the foothills conditions are rather different. Here the altitude is greater, and there is a local relief of 15 or 25 meters. Instead of a simple plain the countryside consists of a pocked and dissected plateau. The surface of this plateau is covered with cottongrass tussocks rather than polygonal ground.

Set about 15 meters into the plateau are occasional stream valleys and many thaw lakes. At present most of the lakes do not completely occupy their basins, so that there is a certain amount of ground as well as water occupying the lower level 15 meters below the surface of the tussock-covered plateau. On this low ground a polygonal pattern has developed, but all the polygons are low-centered young ones.

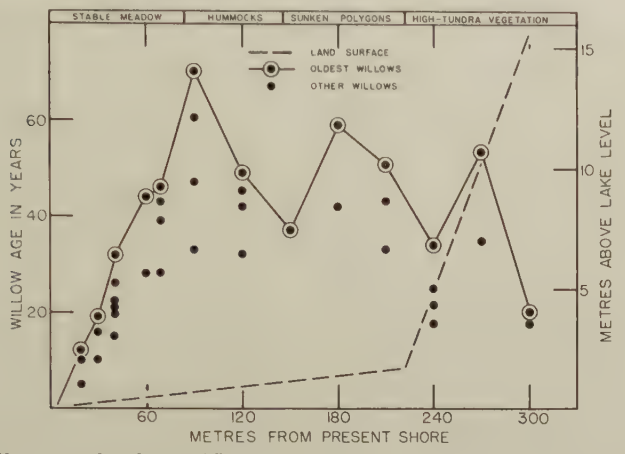

FIG. 3. Age of willows on the shore of East Oumalik Lake as a function of distance from the edge of the water.

An indication of just how young some of this young surface is can be obtained from an analysis of the age of willow shrubs growing on it.

A series of willow shrubs was collected along a transect of the low plain along the west shore of East Oumalik Lake (69° 50′ N, 155° 27′ W). The age of the shrubs was determined by counting the annual rings, and the age of the plants was then plotted against their distance from the water's edge (Fig. 3). For the first 90 meters the age of the oldest willow at each sampling station bears a direct relationship to the distance of the station from the water. Apparently the level of the water has been gradually falling, and the age of the shrubs growing on any spot is dependent upon the length of time since the spot was uncovered by the retreating lake.

Farther away from the shore the straight-line relationship breaks down completely for reasons that were obvious in the field. Beyond the 90-meter station the ground is broken up into polygons, and willow bushes are scarce. The few that do occur have a precarious existence on the dykes dividing the low-centered polygons, where they are at the mercy of frost-churning which kills them before they reach a very great age.

If we extrapolate the rate of lake retreat indicated for the stable ground near shore over the entire distance from the present water's edge to the steep bank where the water stood when the lake occupied its basin completely, we arrive at a figure of 150 years, more or less, for the length of time since the lower level of the landscape was exposed by the retreating lake. Some parts of the lake basin may be somewhat older than this, but such rapid evolution suggests that East Oumalik Lake is rather young. Apparently lake formation in the transition zone around East Oumalik is a rather recent phenomenon. Around Point Barrow, on the coastal plain proper, it has been going on for a long time.

The bottom profile of East Oumalik Lake (see Figs. 1 and 2) shows its youthfulness. Over most of the lake smooth contours are prevalent, as they are over all of Ikrowik. In the northern part of the Oumalik basin, however, there are numerous deep pits. These pits all occur in the vicinity of rapidly eroding parts of the shoreline. They are in the part of the lake that appears youngest and almost certainly are the cavities left by melted ice wedges. Such ice wedges are exposed at several places in the Oumalik neighborhood.

The growth of East Oumalik Lake appears to have proceeded in steps. Each step consists of a stage of active growth, during which ice wedge holes appear in the lake bottom, then a period of quiescence, during which the contours are smoothed out. At the present time the lake is in an active phase and is expanding toward the north. It must be admitted that if the active phases are short and the quiescent phases long, then

the lakes may be much older than is indicated by the ages of the willows on the shore at East Oumalik. The foregoing computation, which yielded a figure of 150 years, probably deals only with events during the current active phase.

If we assume that lakes form at random over the countryside, the lake bottom contours give us a means of estimating the amount of ground ice contained in the upper layers of the country material. Consider the volume contained by the surface area of East Oumalik Lake between the level of the plateau and the level of the deepest hole in the bottom. At the present time this volume is occupied by air, water, and silt. Before the formation of the lake it was occupied by silt and ice. Very little of the original silt has left the basin, because of the depth of the lake and the weakness of the drainage from it. At present there is no outlet stream at all, but there is physiographic evidence that in former times when the lake level stood higher, water did spill over into a small brook joining the Oumalik River. This stream can scarcely have removed much silt from the basin, but it may have removed a good deal of water. More water may, of course, have evaporated.

At the present time, then, silt occupies about the same fraction of the total volume that it did before formation of the lake. The original ice has been replaced by the water in the lake and by the air above it. These various volumes computed from the contour map with the aid of a planimeter indicate that about 70 per cent of the volume was originally occupied by ground ice:

Height of plateau above water	16 m
Maximum depth of water	12 m
Total depth of basin	28 m
Surface area of original lake	1.93×10^6 m^2
Total volume	54.04×10^6 m^3
At present, air volume is	30.88×10^6 m^3
water volume is	6.00×10^6 m^3
mud volume is	17.16×10^6 m^3

Original ice volume = present water volume + present air volume = 36.88×10^6 cubic meters

Original ice volume as percent of total volume = $\frac{36.88}{54.04} \times 100 = 68\%$

This proportion is rather high but not surprisingly so. Casual observation of the amount of ice exposed in cut-banks and slump scars indicates that it is of the correct order of magnitude. Although subject to various errors it probably provides the best estimate of ground-ice volume that is currently available—a much better estimate than core-drilling, for example, which covers a much smaller volume and is apt to melt some of the ice while the sample is being taken.

These actively-growing lakes fill a role that is rather unusual for small bodies of standing water. They are the most effective erosional agents in the district and are rapidly reducing the countryside to a local base level about 15 meters below the top of the plateau. One tends to think of small lakes as passive and temporary basins of sedimentation; it is rather surprising to find them actively devouring the landscape in this way.

Morphometric data also provide one character that usually distinguishes thaw lakes from kettles. The important difference is in the size of the holes left when ice masses melt. Coalescence of ice-wedge holes may produce a basin many miles in extent, but the individual pits are only about ten meters in diameter. In an active ice-wedge lake these pits are easily detected with the sounding line, although they are too small to show up on a map of ordinary scale. Most kettle-holes are much more than ten meters in diameter, and so kettle lakes lack this pattern of fine bottom pitting.

Before leaving the difference between kettles and thaw lakes it would be well to draw attention to two of the ways in which the erosional processes of permafrost regions can modify the morphology of a real kettle. White Lake, in the Brooks Range, lies in a till body of Itkillik (Early Wisconsin?) age (Livingstone 1955b, Péwé *et al.* 1953), so that, barring a very exceptional lingering of a buried ice mass all through the mid-Wisconsin interval, it must be a very old kettle. Yet a considerable amount of mudflowing is taking place on its banks (see Fig. 4). This erosion produces a series of cusps between the scars of successive mudflows that might, after the passage of a few centuries, be confused with crevasse fillings. In this way the sculpturing of the shores of a kettle may

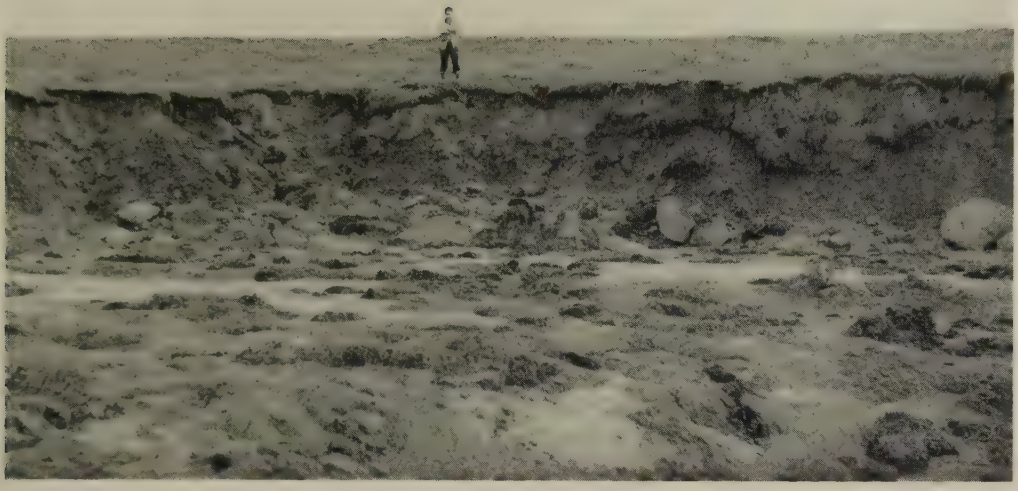

FIG. 4. An active mudflow on the shore of White Lake. View looking east to the slump scarp at the source of the flow.

be rejuvenated every time the climate becomes cold enough for the establishment of permafrost.

While it is rejuvenating the visible parts of the kettle this process may mask part of the sedimentary record. The silt, sand, and gravel delivered to the lake by mudflow may be distributed over the bottom and might form a layer impenetrable to standard sediment samplers. A mild example of this sort of thing is, of course, very well known from the Upper Dryas deposits of western Europe. What we have in mind is a much more severe development of solifluction, leading to the formation of a deposit massive enough and coarse enough in texture to be confused with basal till.

PHYSICAL LIMNOLOGY

The characteristic features of the physical environment of an arctic lake are its low temperature and the extreme seasonal variation in insolation. Because our field work was restricted to the summer months, information is lacking about the interesting long winter night with its thick ice cover. Dr. Wiggins of the Arctic Research Laboratory at Point Barrow very kindly measured the ice thickness of Ikrowik during the spring of 1951, but even this elementary datum is missing for most of the lakes. The depth of spring ice on Ikrowik, however, was 1.85 meters, which indicates a considerable depth of freezing for lakes in the area.

Some summer temperatures are available (see Table 1), and since most of them were obtained during August they can be accepted as an approximation to the maximum temperature attained during the year.

The first thing that is apparent from the available temperature data is that no arctic lake examined shows summer stratification. It is unfortunate that stormy weather prevented temperature measurements on White Lake, which is over twice as deep as the deepest temperature record in Table 1. Perhaps this lake does show some summer stratification, but the others, even Chandler Lake at 18 meters (temperature readings

TABLE 1. *Water and mud temperatures of some Alaskan lakes*

Chandler Lake, Aug. 15, 1951		East Oumalik Lake						Imikpuk, Sept. 1, 1952	
		July 26, 1951		near middle Aug. 15, 1951		near shore Aug. 16, 1952			
Depth m	Temp. °C	Depth m	Temp. °C	Depth m	Temp. °C	Depth m	Temp. °C	Depth m	Temp. °C
Air	15.40	Air	13.32	6	12.0	Into the mud		1.00	4.40
Surface	9.54	Surface	13.07	10	10.0	3	11.3	2.00	4.35
1	9.70	1	13.04	Into the mud		3.25	10.2	2.25	4.35
2	9.52	2	13.01	10.25	8.8	3.50	8.7	2.50	4.35
3	9.34	3	12.98	10.50	7.4	3.75	7.3	Into the mud	
4	9.42	4	12.98	10.75	6.4	4.00	6.4	2.75	4.28
5	9.36	5	12.94	11.00	5.9	4.25	5.2	3.00	4.10
6	9.30	6	12.94	11.25	5.1	4.50	5.1	3.25	3.83
7	9.20	7	12.93	11.50	4.8			3.50	3.37
8	9.14	8	12.87	11.75	4.7			3.75	2.85
9	9.15	9	12.83	12.00	4.2			4.00	2.48
10	9.10	10	12.72					4.25	2.39
11	9.08								
12	9.07								
13	9.07								
14	9.05								
15	8.94								
16	8.83								
17	8.80								
18	8.76								

were not taken in the 21-meter hole of Chandler) and the small 12-meter pit in East Oumalik Lake, were circulating. This is not very remarkable, although temperate lakes of similar size and shape would be expected to show some stratification. The deep Alaskan lakes attain a summer temperature of only 12 or 13°C. They warm through the range of slight density change of water, and only a moderate amount of work is required to mix the warmed surface water into the depths. Because the lakes are unprotected by trees the summer wind is in an ideal position to perform this moderate amount of work.

The work of the wind in distributing water warmed above 4°C has been calculated for Chandler Lake by the method of Birge (1916). It is 175 cal/cm^2 of Lake surface. This is to be compared to a value for Lake Mendota in Wisconsin, a lake of comparable depth, of 1209 cal/cm^2. The difference is not due to the strength of the prevailing summer wind, which is much greater in the Brooks Range than it is in Wisconsin, but simply to the low summer temperature of the Brooks Range.

In the absence of good winter temperature data, and especially of data on the thickness of ice, it is impossible to construct an accurate heat budget for Chandler Lake. By making a few reasonable assumptions about the state of affairs in winter, however, we can calculate a rough heat budget that will not be too far from the true one. Suppose we assume a depth of freezing of two meters and assume further that the upper meter of this ice is cooled to a temperature of -10°C, while the lower meter is cooled only to 0°C. No data are available for the water temperature at the time of freezing, but it will be less than 4°C throughout the lake and probably, because of the very high winds, quite close to 0°C.

Accepting these assumptions, the heat budget of Chandler Lake is as follows:

warming above 4°C	864×10^{12} cal
warming, 0–4°C	660×10^{12} cal
melting 2 meters of ice	2480×10^{12} cal
warming upper meter of ice	150×10^{12} cal
total heat income	4154×10^{12} cal

Dividing total heat income by the surface area of 15×10^{10} cm^2 we get 27,800 cal/cm^2 of which 5800 cal is wind-distributed heat.

It is evident that the largest item in this

budget is one of the least secure, but even if the ice were as thin as one meter, which is most unlikely, the wind-distributed heat would still represent less than a third of the heat budget. This is a very small percentage by temperate zone standards. Even in Lake Ladoga, the most extreme of the lakes listed by Birge (1915), wind-distributed heat accounts for over half of the heat budget.

Note that this lake, although it lies well within the Arctic Circle and at an altitude of almost a thousand meters, is still a temperate lake according to the classification of Forel (1901). By his scheme only lakes which never rose above 4°C were to be considered polar. Andersen (1946), working in northeast Greenland, also found that his lakes warmed up to about 12°C, and it appears that most arctic lakes would fall in the temperate category of Forel. His scheme of classification is, nevertheless, an elegant one, and there is no disputing the fact that failure to attain 4°C is an important physical characteristic. Hutchinson and Löffler (1956) have recently removed the difficulty by using the latitudinally neutral terms cold monomictic, dimictic, and warm monomictic for the three categories of Forel. In our experience arctic lakes have been "temperate" or "dimictic" ones, too shallow to stratify in summer, in which the wind-distributed heat is less than half of the heat budget, and we suspect that this may be generally true of lakes in the polar regions, except for the handful of cold monomictic ones.

The thickness of the winter ice has a profound effect on the thermal balance of the basin in which a lake lies. Dry land in arctic Alaska is underlain by perennially frozen ground and the same is true of land covered by shallow water. Lakes too deep to freeze solid in winter, however, have a bottom temperature that is above freezing throughout the year. Should such a lake form over frozen ground there is a flow of heat from the water to the mud so that a body of unfrozen ground accumulates. Ultimately an equilibrium condition results in which the body of unfrozen ground is as large as can be maintained by the heat flux through the bottom, and the temperature of the upper layers of mud rises and falls with seasonal change in water temperature.

Table 2. *Color and transparency of some Alaskan lakes*

Lake	Date	Secchi depth m	USGS color ppm	Forel-Ule color
Eight Lake	Aug. 22–23, 1951	3	15	XXI
Lake A	July 27, 1952	3		
Ikrowik	July 1, 1951	2	25	XXI
East Oumalik Lake	July 26, 1951	2.7	5	V
Chandler Lake	Aug. 9–11, 1951	5	15	VI

We have a few data concerning the extent of the unfrozen ground. Chandler Lake sediments, under 21 meters of water, are thawed to a depth of at least 7 meters, and East Oumalik Lake sediments, under 12 meters of water, are thawed to a depth of at least 4 meters. In Skimo Lake near Barrow Village, with one meter of water, solid ice persists in midsummer less than one meter below the mud-water interface. Presumably the sediments of such a lake are completely frozen during the winter, and this presumption is borne out by the fact that a well-developed polygonal pattern beneath the shallow water is visible from the air.

It should be noted that the net flow of heat from the water to the mud in deep arctic lakes is in accord with such data as are available for temperate lakes. Birge, Juday, and March (1928) found that there was a slight but appreciable net transfer of heat from the water to the mud of Lake Mendota in the course of a year.

A less important effect that the ice of an arctic lake exerts on its basin is that of ice-push. This is a phenomenon to be found in the temperate zone wherever there is severe freezing in winter, but in arctic lakes it is quantitatively more important and is one of the dominant processes sculpturing the beaches. On the lakes of the Chandler River system exposed deltas have ice-push ridges four or five meters high which are so substantial they are not reduced even by the heavy gales of summer.

Because of the thermal capacity of a deep lake the ice cover forms in the fall and disappears in the spring more slowly than it does on shallow ones. This must be of considerable importance in the illumination of

the water, for it keeps the deep lakes ice-covered until July. More than half the season of 24-hour sunlight has passed by the time the ice disappears. The millions of separate crystals of melting spring ice reflect a good proportion of the incident light, and this must have a very great effect on the annual light income of the deep lakes.

Such color and transparency data as are available are presented in Table 2. It may be seen that the transparency was neither very great nor very variable. Measurements were not made on a thaw lake while it was circulating under a strong wind. Under such circumstances many thaw lakes are very turbid and the transparency might be much lower. Color is extremely variable, even in the small series of lakes examined. The shallow lakes tend to be brown, many of them, like Ikrowik, rather deeply stained, while the deep lakes are (lightly) colored a characteristic translucent gray-green. This color never failed in our experience as an indicator of considerable depth.

CHEMICAL LIMNOLOGY

Chemical tests for a few major ions were carried out in the field. In addition, samples of unfiltered water were collected in pyrex bottles and sent to Dr. Whetstone, Alaska District Chemist, who analyzed them within six months. His results, which are more reliable than the field tests, are presented in Table 3.

TABLE 3. *Chemical analyses of some Alaskan lakes (in ppm)*

	East Oumalik Lake, July 26, 1951	Small lake NE of East Oumalik Lake, July 28, 1951	Chandler Lake August 22, 1951	Eight Lake August 22, 1951	Ikrowik	
					June 30, 1951	July 13, 1951
SiO_2	1.0	1.9	0.4	1.9	0.0	0.9
Fe	0.04	0.01	0.03	0.01	0.05	0.01
Mn	0.00	0.00	0.00	0.00	0.00	0.00
Ca	31	39	5.6	6.0	2.5	5.9
Mg	9.4	7.4	3.2	3.4	1.9	3.9
Na + K	8.0	4.6	2.5	6.0	7.0	18
CO_3	0	tr	0	0	0	0
HCO_3	122	146	24	34	8	12
SO_4	3.2	5.4	9.1	13	2.4	4.1
Cl	21	8.5	1.5	0.1	14	40
F	0.1	0.1	0.4	0.1	0.1	0.1
NO_3	0.4	0.3	0.4	0.3	0.3	0.2
PO_4	0.0		0.0			
Dissolved solids	159	139	40	48	35	82
Total hardness as $CaCO_3$	116	128	27	29	14	31
Specific conductance (micromhos at 25°C)	271	246	66.9	63.4	68.2	159
pH	7.2	7.8	6.6	4.7	6.8	6.9

Chemical tests for a few major ions were carried out in the field. In addition, samples of unfiltered water were collected in pyrex bottles and sent to Dr. Whetstone, Alaska District Chemist, who analyzed them within six months. His results, which are more reliable than the field tests, are presented in Table 3.

The most obvious generalization that can be drawn from the results is that Ikrowik, which is only seven km from the coast, is predominantly a sodium chloride lake, while calcium and bicarbonate ions predominate in the inland lakes, with lesser quantities of magnesium and sulphate.

The two analyses of Ikrowik water span the period of disappearance of the ice. We expected that the summer water would be more dilute than the spring water because of the addition of relatively pure ice meltwater. Apparently the blown sea-spray of summer is sufficient to nullify the effect of meltwater and make the summer water more concentrated than the water is in the spring.

East Oumalik Lake and the small lake northeast of it are substantially more concentrated than the others. East Oumalik Lake is without an outlet, but since the other is a drainage lake the high concentration cannot be the result of evaporation. Presumably it is due to bedrock control.

Chandler Lake and Eight Lake are rather high in sulphate. This, too, is probably the result of bedrock control, but we cannot substantiate this belief with analyses of the bedrock in either case.

It is evident from the table that the water chemistry of these Alaskan lakes is not extraordinary. The only feature that may have regional significance is the low silica content. Silica analyses of waters stored in glass bottles are notoriously unreliable, and it may be worth while to note in this connection that we were unable to detect silica in any of our field tests, using a Taylor comparator and a method sensitive to one milligram per liter. The silica-sesquioxide ratio of cold-climate soils is high (Robinson 1936), and it is to be expected that the waters leach-

ing such soils would be low in silica. The observations of Böcher (1949), however, who found several parts per million of silica in dilute Greenland lake water after it had been stored in glass for many months, prevent us from generalizing to any great extent about the silica content of arctic waters.

BIOLOGICAL LIMNOLOGY

The most striking biological characteristic of arctic Alaskan lakes is the absence of a well-developed shore community. In the smaller lakes there is sometimes a good stand of *Arctophila fulva*, a coarse aquatic grass, and in the shallow ponds there is often a good growth of *Hippuris vulgaris* or *Ranunculus pallasii*. Spetzmann (1951) lists a total of only thirteen species of vascular plants from aquatic communities on the North Slope. In general, though, the dense stands of emergent and floating vegetation that are found around the shores of so many temperate zone lakes, particularly shallow ones, are lacking in most lakes of northern Alaska.

The great variety of animals usually inhabitating the shore zone of lakes is missing too. There appear to be no freshwater sponges, no Notonectidae, Corixidae, Gyrinidae, Dytiscidae, and no Amphibia north of the Brooks Range. The lack of a shore community, combined with the scars of heavy ice-push, gives to even the most permanent arctic lake a barren, raw, and temporary aspect. The shoreline looks like that of a spring puddle or temporary ditch rather than a lake.

It is not easy to determine the reasons for lack of a shoreline community. Undoubtedly the ice plays an important role. The mere physical disruption which it causes must inhibit the formation of a proper community, just as heavy wave action does in the temperate zone. It is evident, however, that this is not the whole story. On the south side of the Brooks Range, where winter temperatures are almost as low as on the north slope, but where the summer is much warmer, many of the elements of a shore community are present. At Death Valley near Bettles, for example, both Notonectidae and Gerridae were observed. Although no living sponges were seen spicules are common in the sediments of this lake. At Bettles there are frogs (personal communication from Mr. James Bee), and in all the lakes of the vicinity there is a dense growth of water lilies (*Nuphar* sp.). It appears that some of these species are being governed in their distribution by the same factors that govern the distribution of the timberline. Summer temperature is particularly likely to be important in the case of poikilothermous animals.

It should be noted that although lack of a shore community is characteristic of most lakes on the tundra we cannot say with assurance that all lakes with an arctic thermal regime will be without one. Although the necessary data on summer temperature and thickness of winter ice are not available, it seems likely that Death Valley Lake and others like it in the interior of Alaska which have a well-developed shore zone would be classified as arctic on the basis of the thermal scheme proposed above.

Whether or not a lake freezes to the bottom in winter is, of course, a matter of very great biological importance. Fish, in our experience, are to be found only in lakes that are deep enough to have a considerable body of water under the ice in winter, or else in lakes that are connected with deep lakes, rivers, or the sea. It is widely believed that the Alaskan blackfish, *Dallia pectoralis*, is able to withstand freezing, or at least temperatures below the freezing point of pure water (Jordan and Evermann 1896, p. 621). Attempts to verify this in the laboratory have failed consistently (Scholander *et al.* 1953).

At East Oumalik many sticklebacks (*Pungitius pungitius*) were found in small pools and tractor ruts on the floodplain of the lake. It was apparent from the location of these ruts and puddles that the fish could have reached them at any time the water level was raised by a few decimeters, or at any time snow meltwater was flowing into the lake. The surface of the tundra is wet at all times and well provided with pools and puddles. Small fish such as sticklebacks and young blackfish would have little difficulty moving across it from deep lakes to

TABLE 4. *Net weight of dredgings from some Alaskan lakes*

	Depth of dredgings m	Sphaeriidae g	Tendipedidae g	Oligochaeta g	Gastropoda g	Miscellaneous	Total g	Total weight g/m²	Weighted mean for entire lake kg/ha
Chandler Lake (mean depth 11 m)	14	0.000	0.017	0.000	0.000	Copepoda, cyclic diatoms, Ostracoda, ephippia	0.017	0.85	
	14	0.010		0.000	0.000	Cyclic diatoms, ephippia, oligochaete cocoons	0.010	0.50	6.99
	21.5	0.010	0.016	0.011	0.000	Copepoda, ephippia, oligochaete cocoons	0.037 0.037	1.85 1.85	
	21.5	0.004	0.005	0.029	0.000	Insect cases	0.038	1.90	
Little Chandler Lake (mean depth 6.3 m)	12 12	0.002	0.032	0.000	0.000	Nematoda, insect cases	0.012 0.034	0.60 1.70	11.5
Lake A (mean depth 3.5 m)	6 6	0.001 0.001	0.024 0.012	0.000 0.000	0.000 0.000		0.025 0.013	1.25 0.65	9.5
East Oumalik Lake (mean depth 3.1 m)	12						0.025	1.25	
	10.5	0.054	0.007		0.007		0.068	3.40	
	4	0.004	0.046	0.000	0.052	Characeae, insect cases	0.102	5.10	
	4	0.123	0.242	0.009	0.004	Ostracoda, Hydracarina, Nematoda	0.378	18.90	89.4
	1	0.083	0.005		0.080	Musci, Characeae, gelatinous algae, insect cases	0.168	8.40	
Ikrowik (mean depth 2 m)	2	0.000	0.000	0.000	0.000		0.000	0.00	0.0

shallow ponds where their presence would be cause for surprise. It is, of course, possible that these fish may be able to withstand freezing temperatures, but until such time as they have survived freezing in the laboratory or been collected alive in the ice it is not wise to accept the circumstantial evidence of occasional occurrence in shallow ponds.

However it may affect fish, Andersen (1946) found that winter freezing had no adverse affect on the chironomids of northeast Greenland. On the contrary, there was a heavier population in the shallows, where the animals were submitted to annual freezing, than in the deeper water, where they were submitted to the effects of oxygen depletion while in an active state.

In Alaska there does not seem to be any such enhancement of the bottom fauna in the shallows. Although a fertile lake such as East Oumalik maintains a good population of bottom animals in the one-meter zone, the crop is even heavier in water of moderate depth. This difference is probably due to the greater size and consequent greater ice-push of the Alaskan lakes. Eight Lake, the only one comparable in size to Andersen's, was not dredged for bottom animals, but it had, as already mentioned, a fair amount of rooted vegetation in the shallows. On large lakes the physical disruption due to ice expansion probably prevents the establishment of a good bottom fauna in the littoral zone, just as it prevents the establishment of a shore community generally.

Prescott (1953) found considerable difference in the algal floras of the various thaw lakes near Point Barrow. A particularly striking difference is that between the acid

desmid-dominated lakes and the basic diatom-dominated ones. Failing to find any consistent chemical differences other than pH between the two types of lakes Prescott suggested that accidents of colonization might be responsible for the floral differences. To the present authors it seems rather likely that a chemical difference involving some ion or ions not measured by Prescott does exist and that the differences are due to the chemical composition of the sediments in which the lake basins lie.

This part of the coastal plain has had a very complicated Pleistocene history. After any good August gale when the sea cliffs are well exposed, the churned and interfingering layers of terrestrial, aeolian, marine, lacustrine, and fluviatile material that compose the upper part of the Gubic formation around Point Barrow can be seen. As mentioned above, the surface of the coastal plain bears witness to a very complex history of lake formation, drainage, and reformation, so that various lakes on the coastal plain are apt to have had very different histories and be surrounded by materials of very different chemical nature. A lake that is actively eroding a shallow calcareous sea deposit will have a different water chemistry from one that is expanding into windblown sand or one that is shrinking.

One chemical substance not measured by Prescott that seems to us very likely to be involved in the difference between a diatom flora and a desmid flora is silicon. Lund (1950) has shown for *Asterionella* that 0.5 ppm of silicate is essential to growth. Nonplanktonic species probably require considerably more than this. Hutchinson (1957, pp. 797–8) cites a number of laboratory investigations in which diatoms were found to grow best at concentrations up to 30 ppm of silicate. It may be significant, therefore, that Ikrowik, the only lake we have both worked on, was found by Prescott to have no diatoms at all and by us to have too little silicate to be detected by our field method.

The results of dredgings taken in a variety of lakes are summarized in Table 4. The bottom fauna is low, but not remarkably so. The data for these lakes when plotted against mean depth on a graph with data from a large number of lakes, such as that of Deevey (1941), fall near the bottom of the range of scatter but do not appear to form a separate group. This is in agreement with the findings of Comita and Edmondson (1953) who concluded after an intensive study of the productivity of Imikpuk near Point Barrow that the summer productivity and the summer standing crop of the lake did not differ markedly from those of temperate lakes. A great deal of solar energy enters a high latitude lake during the summer. It is the shortness of the growing season that limits the annual production of arctic lakes.

PALEOLIMNOLOGY

Gross stratigraphic features

Conditions of sedimentation in arctic lakes are under the close control of climate and its associated physiographic processes. It is evident from what has been said about the origin and development of thaw lakes that the sediments laid down in an actively expanding thaw lake are derived in very large measure from the silt and peat of which the banks are composed. For this reason it is difficult, if not impossible, to apply the standard stratigraphic methods to the investigation of thaw lake history. The chemistry and fossils of the sediments that have been deposited on the lake bottom are very likely to have been derived from older beds surrounding the lake basin. What is more, in most cases it is impossible to separate such derived fossils from autochthonous ones.

The danger of secondary deposition was underlined in the summer of 1951, at East Oumalik Lake, when the bones of an extinct elephant were found lying on the surface of the lake mud a short distance from shore. The bones were disarticulated fragments, and even if they had been found deeper in the sediment they would not have been accepted as indicators of conditions at the time the bone-bearing bed was laid down. There is no obvious way, however, in which cladocera, tendipedids and pollen grains washed out of old lake deposits in the shore can be discriminated from the much younger

fossils of organisms that lived during the lifetime of the present lake.

A further difficulty is to be found wherever lakes lie in an unconsolidated formation that is itself partly lacustrine in origin. It is impossible, in taking the core samples, to know when one has pierced through the sediments of the present lake and entered the underlying beds of some extinct lake that may be many thousands of years older.

In the rocky basins of the Brooks Range we always knew when we had penetrated the lake sediments: further progress was impossible. Out on the coastal plain, with its thick unconsolidated mantle, there was no way of telling when the bottom of the lake deposit had been reached. It is quite possible that the cores taken in the deepest part of East Oumalik Lake, in the recently thawed ice-wedge pits, did not go through sediments of the present lake at all, but only through the underlying Gubic formation.

Because of this difficulty in deciphering the fossil record of the coastal plain lakes, consideration will be restricted to the glacial lakes of the Brooks Range.

Pertinent observations were made on four lakes in the mountains: Death Valley Lake near Bettles; Chandler Lake north of the Brooks Range divide; and two smaller lakes near Chandler Lake, Eight Lake and Lake A.

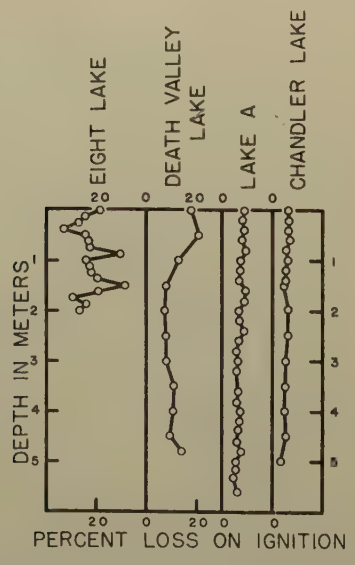

FIG. 5. Percent loss on ignition of lake sediment.

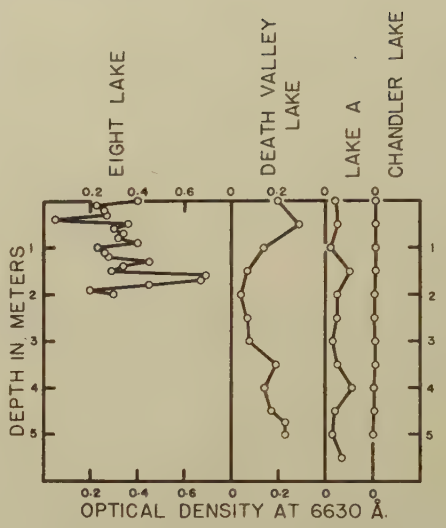

FIG. 6. Chlorophyll content of lake sediment.

The time scale used in the paleolimnologic computations is based upon pollen analysis of cores from the lakes. The detailed results of these analyses have already been published (Livingstone 1955b). For present purposes it is sufficient to state that three pollen zones can be recognized in the longest profile, from Chandler Lake, but only the upper two of these can be recognized in the other lakes. These zones, which have been arbitrarily designated I, II, and III, consist of an herbaceous pollen zone, a birch pollen zone, and an alder pollen zone, respectively. Three of the lakes are so close together that the II/III transition, the only identifiable horizon found in all three sections, is certainly synchronous in these lakes. Death Valley Lake is so far away, however, and situated in a region of such different climate and vegetation, that there is every likelihood that its II/III transition is not synchronous with that in the Chandler region, but dates from a much earlier time.

Undated pollen zone boundaries are of limited usefulness in dealing with the history of lakes. Unfortunately the organic content of most of the Brooks Range Lakes is so low as to make direct carbon dating difficult, so one is forced to rely on correlations with the nearest carbon-dated pollen

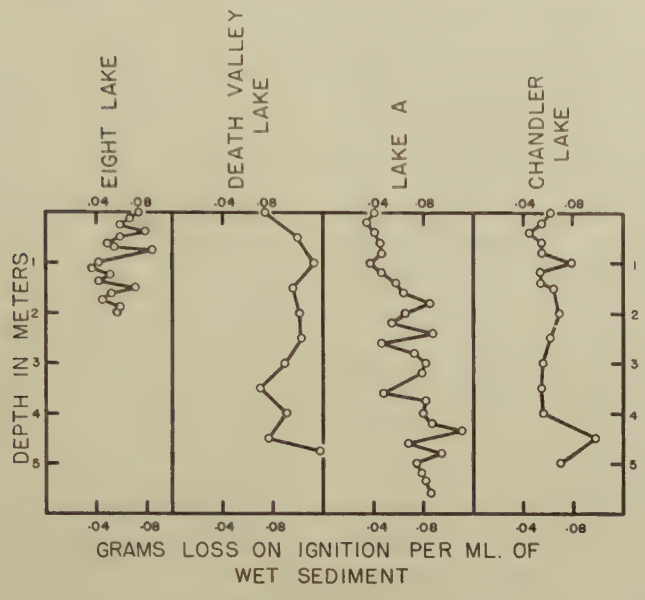

FIG. 7. Organic content of lake sediment.

profile, from a valley fill near Umiat, 134 km to the north of Chandler Lake (Livingstone 1957a). This profile consists of three pollen zones. The upper two correspond vegetationally to the upper two at Chandler, and as the distance and vegational difference between these two localities is not great, it is very likely that the II/III boundary is synchronous or nearly so at Umiat and Chandler Lake. At Umiat this boundary has a carbon age of 5900 ± 200 years.

The lowest zone at Umiat bears many similarities to Zone I at Chandler Lake but it also has some important differences, mainly the presence of a considerable amount of birch pollen throughout the zone. For this reason some considerable doubt arises about the synchrony of this transition with the I/II transition at Chandler Lake, but nevertheless the carbon age of between 7500 ± 250 and 8100 ± 250 years may be taken as an estimate of the age of the I/II transition at Chandler Lake. This estimate is likely to be too low if the Umiat Zone I is, as its high birch content suggests, contemporary with Chandler Zone II instead of Chandler Zone I.

Organic and inorganic matter

Per cent-loss-on-ignition curves have been drawn in the conventional manner for the four mountain lakes (Fig. 5). These curves are rather featureless, and, with the possible exception of Death Valley Lake, lack any indication of the dramatic sigmoid increase in organic content apparently typical of temperate-zone lakes (Hutchinson and Wollack 1940, Deevey 1942). It is the opinion of one of us (Livingstone 1957b) that the sigmoid increase of temperate zone lakes is a result of the change from arctic to temperate weathering conditions, a change that has not yet occurred in northern Alaska, so one would not, perhaps, expect to find a sigmoid increase in our three northernmost lakes nor more than a very questionable indication of it in our subarctic lake from Death Valley.

Some explanation can be offered for the differences between the loss on ignition curves of the various lakes. Chandler and Lake A have similar curves: loss on ignition is low, and it undergoes a slow but steady increase from bottom to top of the section. The sediment in these lakes is only to the smallest degree autochthonous. It is clayey

silt, brought in by viscous creep and stream action. The source of this material is the thin active layer, a few decimeters thick, that thaws out in summer and slides slowly over the smooth underlying frozen substratum of the countryside to the depressions containing the lakes and streams. The material of which this mantle is composed is clayey silt with some included peat, and it bears on its surface the living tundra vegetation.

At Death Valley the delivery of material by viscous creep is not so important. The sediment filling the lake is a silty gyttja. A certain amount of allochthonous material is being added to the lake, however, by localized thawing and slumping of the shores.

Eight Lake does not receive such massive amounts of allochthonous material from any source at the present time. It lies in a rocky till-body, where viscous creep is not active, and its shores are not slumping nor do they bear recognizable slump scars. A small stream enters it, and this probably accounts for a considerable percentage of the small amount of inorganic material entering the lake basin.

A rough estimate of the chlorophyll content of the sediment in the four lakes was obtained by extracting samples of sediment in acetone and measuring the optical density of the solution. The results are plotted in Figure 6. The curves bear a general similarity to the ones for per cent-loss-on-ignition, with the principal difference being the extremely low chlorophyll content of Chandler Lake sediment.

This difference is due in part to a relatively small contribution of chlorophyll-rich autochthonous organic matter and a relatively large contribution of peaty terrestrial material to the total loss on ignition for Chandler Lake, but it may partly be due also to a more severe mineralization of the settling seston in Chandler Lake, which is much deeper than the others.

Per cent-loss-on-ignition curves are apt to be rather misleading, for they are influenced by changes in the rate of organic sedimentation and also changes in the rate of mineral sedimentation. They make no allowance for differences in the water content of the sediment. Thus the loss-on-ignition curves might indicate that the organic content of Eight Lake sediment was much higher than that of any of the other lakes, but when the data are plotted in terms of grams lost on ignition by each cubic centimeter of sediment, as in Figure 7, a rather different result emerges. On this basis the four lakes are rather similar. Per cent loss on ignition is a function of both mineral content and organic content and the differences in per cent ignition loss between these lakes result from differences in mineral content (see Fig. 8). Eight Lake, except at 0.4 meters, has an unusually low mineral content by arctic standards. Much of the sediment volume in this lake is composed of water. Viewed in this light the difference in chlorophyll content of the lakes appears even more striking.

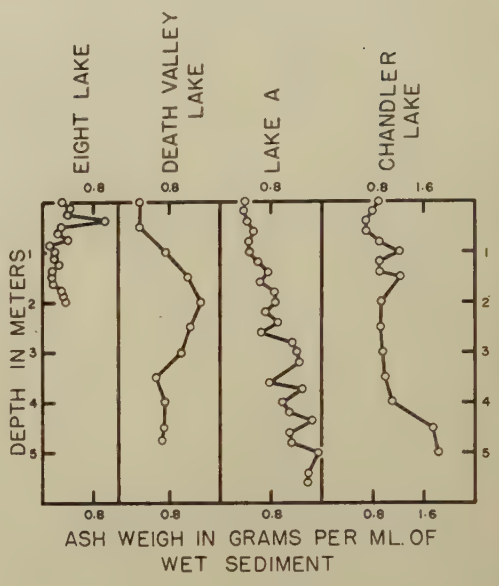

FIG. 8. Ash content of lake sediment.

Microfossils

Of the Chandler lakes only Eight Lake was rich in morphological fossils. Tendipedid (chironomid) head capsules, jaws, and exuviae, including many specimens of *Dryadotanytarsus* and "*Tanytarsus*" (*i.e.*, one of the Calopsectrini), were abundant, as were fragments of *Bosmina* carapaces and turbellarian cocoons. Desmids (*Cosmarium*, *Euastrum*, *Staurastrum*, *Desmid-*

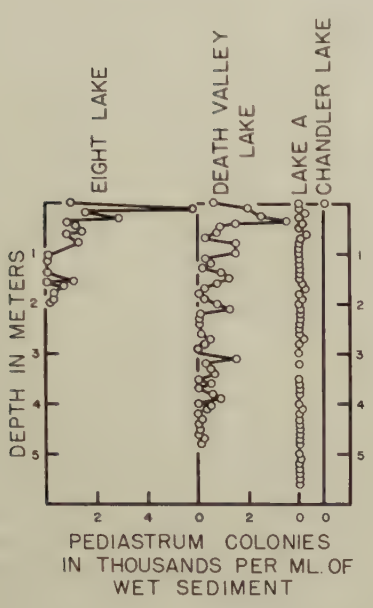

FIG. 9. *Pediastrum* content of lake sediment.

ium), filamentous algae (cf. *Stigeoclonium*), in some levels with recognizable cytoplasmic constituents still intact, and brown moss leaves were also present. *Pediastrum boryanum* was common, especially in the upper levels, and a few pennate diatoms were encountered.

The other lakes also contained *Pediastrum boryanum*, though in smaller quantities. Lake A had a measurable quantity of *Bosmina* and tendipedid fragments, but in Chandler Lake tendipedids were very scarce and *Bosmina* was not recognized at all. Death Valley Lake has a rather rich fossil fauna and flora, including diatoms, which were scarce elsewhere, and sponge spicules, which were not encountered at all in the more northern lakes; no detailed counts, however, have been made on its sediments except for things such as *Pediastrum* which are found on the pollen slides.

In all four lakes (see Fig. 9) *P. boryanum* shows an increase from bottom to top, although little significance can be attached to this increase in Chandler and Lake A, where the total numbers involved are very low. It is interesting to note that the highest *P. boryanum* content is found in the shallowest lakes. In further support of this tendency may be mentioned the fact that Footprint Lake near Point Barrow, which contained only about one meter of water until artificially drained a few years ago, laid down a sediment so rich in *Pediastrum* that the colonies cannot be counted by the standard method. *P. boryanum* is an extremely variable species and a tychoplanktont. There is no reason known to the authors for considering it as a plant of shallow waters in general, but it appears to be in Alaska. If this is so then the progressive increase it shows in the sedimentary column of each individual lake may simply reflect shoaling as the lake filled in.

Of other microfossils only Eight Lake has numbers high enough for reliable counting. This lake shows a very striking decline of *Bosmina* carapaces and tendipedid fragments from initial high values to later low values (Figs. 10 and 11). This is the opposite of what one usually finds (Deevey 1942), and taken at face value it indicates a decline in productivity since the early history of the lake. *Pediastrum* shows that the situation is not so simple as this, as do the brown moss leaves that form the bulk of the sediment in the upper 0.4 meters. We are really not justified in drawing a conclusion of diminished productivity from such conflicting evidence.

We may, however, be justified in drawing conclusions about a change in the nature of the material produced, though even here we must be cautious. The decline in *Bosmina*, for example, may not reflect a decrease in

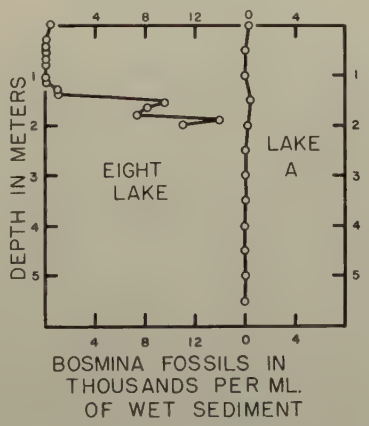

FIG. 10. *Bosmina* content of lake sediment.

overall zooplankton production, but simply a replacement of cladocerans by copepods as dominant members of the zooplankton community. Copepods do not fossilize under ordinary conditions and they were certainly the most important animals in the zooplankton when we visited the lake and took plankton tows. The decrease in tendipedids, however, is not so easily explained by such special pleading, and the general impression that emerges is one of a decrease in the relative amount of animal production. The great increase of mosses suggests that the lake is passing from an initial rather eutrophic condition into a dystrophic one; the brown color of the water at the present time lends support to this suggestion.

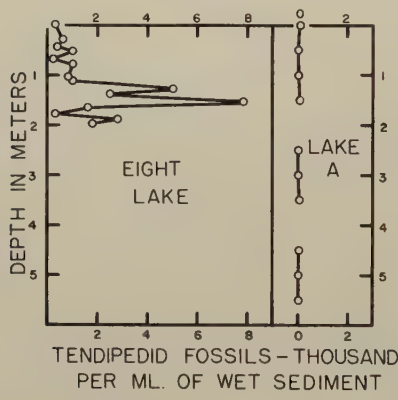

Fig. 11. Tendipedid content of lake sediment.

If this is the case then the peculiar edaphic features of the drainage basin may be involved. Eight Lake lies in a rocky till-body that is free of active mass-wasting of any sort that would expose a continuing supply of fresh soil. In addition, it is perennially frozen below a depth of a few decimeters, so there can be no flow of ground water to the lake. It seems quite likely that under such conditions the supply of mineral nutrients has been drastically reduced since the years immediately after formation of the lake. The connection between dystrophy and dissolved mineral salts is not fully understood, at least by the authors, but it is evident that dystrophy arises under conditions of low base and nutrient content in the water. We do not feel that the occasional examples of moderately calcareous lakes that are dystrophic (Ohle 1934) are sufficient to obscure this general tendency, although they do show that the situation is not a simple one. We offer the suggestion that this lake is becoming dystrophic because of a progressive restriction of the supply of water-soluble mineral substances.

Fig. 12. Lake A, Alaska. View looking north in early August, 1952. Notice how the contours of the tillbody in which this kettle lies have been smoothed by viscous creep. Kames cannot be recognized.

TABLE 5. *Absolute sedimentation rates of Linsley Pond, Conn., and some Alaskan lakes*

	Time interval	Loss on ignition mg/cm²/yr	Ash wt. mg/cm²/yr	*Bosmina* fragments/ cm²/yr	Tendipedid fragments/ cm²/yr
Lake A	Zone III, 6000 yrs	1.66	19.36	6.00	1.2
Eight Lake	Zone III, 6000 yrs	0.88	5.86	0.75	6.6
Chandler Lake	Zone III, 6000 yrs	1.71	24.59	—	—
	* Zone II, 2000+ yrs	4.64	65.45	—	—
Death Valley Lake	*Zone III, 6000+ yrs	6.82	58.52	—	—
Linsley Pond	C-2 & C-3, 5200 yrs	8.31	9.14	6900	2.2
	C-1, 3100 yrs	6.81	6.19	4177	0.7
	† A & B, 3100 (?) yrs	3.94	36.07	433	0.4

* Because of uncertainty about the length of time represented by Zones II and III, absolute sedimentation rates calculated for these zones are likely to be too high.

† Absolute sedimentation rates for Zones A & B may be too high or too low.

Among the microfossils discovered in the sediments of Eight Lake were the head capsules and exuviae of *Dryadotanytarsus*. This genus of midge is known only as a late-Pleistocene fossil. It was described by Andersen (1943) from the Upper and Lower Dryas deposits of Denmark, and found independently by Deevey (1955) in the lake facies of the moa swamp deposit at Pyramid Valley, New Zealand. The Danish species, *D. edentulus*, is restricted in its stratigraphic range to cold-climate deposits, but the New Zealand one, *D. duffi*, is found in temperate deposits, indicating that the genus is not restricted to a narrow range of climate.

We first found *Dryadotanytarsus* remains in the midge rich lower layers of Eight Lake. A systematic search revealed their presence from top to bottom of the core, and so the organism presumably is living in the lake today. This supports the suggestion of Deevey (1957) that the animal is probably known as an adult by some other name.

The rather bizarre feeding apparatus of this midge, with toothless jaws and labium rolled into a tube around the hypopharynx, have given rise to some speculation about its feeding habits. The presence of nucules in both the Danish and the New Zealand deposits prompted the suggestion that it lived by crushing Characeae with the toothless jaws or sucking out their juices with the hypopharynx and labium. The complete absence of nucules from the Eight Lake deposit argues very strongly against a strictly characeous diet, at least for the Alaskan species.

Remains of this midge were not found in any other Alaskan deposit nor in any of the dredgings, despite a keen search for them. Entomologically inclined travellers in the Brooks Range might be well advised to keep an eye cocked for this very characteristic midge and to rear some of the larvae to adulthood if they are found.

We have also found *Dryadotanytarsus* in some material from Whitrig Bog, Scotland, which was very kindly provided for examination by Dr. Anne Conolly. It seems likely that the genus is very widespread as a fossil, and only the unfamiliarity of most palynologists with the Tendipedidae has prevented its discovery in other places.

Dynamics of ecosystem development

Paleolimnologic computations based on estimates per unit volume are basically unsatisfactory because, to translate them into biological terms, one must make some unverified assumption about the rate of sedimentation—usually, that it has been constant. It is much more satisfactory (Livingstone 1957b) to make the computations in terms of time rather than volume of sediment, and for this one must have an absolute time scale of some sort.

The time scale available for the Alaskan lakes is a rather poor one, bearing only two or three gradations of mixed reliability, but it is infinitely better than no absolute time scale at all. In Table 5 loss on ignition, ash weight, *Bosmina* fragments, and tendipedid fragments preserved per square centimeter per year are presented, along with similar data for three sections of the sedimentary column of Linsley Pond. For reasons mentioned above in the section on stratigraphy,

the lengths of time represented by Zone II at Chandler and Zone III at Death Valley are both likely to be seriously underestimated, so that the corresponding rates may be expected to be too high. The length of *A* and *B* time in Deevey's Linsley Pond core L10 is also uncertain, the bottom of the core being equated with Valders time in accordance with some suggestions by Vallentyne and Swabey (1955). The lengths of *C-1* and *C-1* + *C-2* are much more secure, being based on pollen-correlation from the carbon-dated profile of Upper Linsley Pond (Flint and Deevey 1951).

The column listing loss on ignition per square centimeter per year is perhaps of the greatest interest, for rate of deposition of organic material gives a measure of the rate of net productivity of the entire community. Unfortunately, as we have already seen, there is reason to believe that a good deal of the organic matter in the sediments of Chandler Lake, Lake A, and Death Valley Lake is allochthonous and so cannot justifiably be included in the production of the lake. All that can be said about the estimates obtained—1.71, 4.64, 1.66, and 6.82 mg/cm^2/yr—is that they are probably much too high. Chronological uncertainties also make it likely that the figures 4.64 and 6.82 are too high, so we can conclude only that the net community production for these lakes is probably less than 1 milligram per square centimeter per year.

With Eight Lake and Linsley Pond we are on somewhat surer ground. There is no indication of massive allochthonous organic sedimentation, although we must be prepared to expect some influx of wind-blown material, especially leaves, and the figures for these lakes in Table 5 may be taken as first approximations to net community productivity. It is evident that the net productivity of Eight Lake has been lower than that of contemporary Linsley Pond by almost a complete order of magnitude, and that it is even lower than the net productivity of Linsley Pond during the unproductive early stages of its history.

It is not possible to obtain an estimate of past gross production, or even past net plant production, that is independent of the figures for net community production, although there is hope that a careful study of the proportions of stable and unstable components in the sediment may make it possible to arrive at an estimate of changes in diagenetic efficiency. For the time being we must content ourselves with comparing the present-day gross productivity with the net community productivity of the upper layer of sediment.

The light and dark bottle method gives an estimate of the gross productivity of the plankton community in a lake. We did not carry out such determinations in Alaska, but Comita and Edmondson (1953) have reported some determinations carried out on Imikpuk, a lake on the arctic coast at Point Barrow which is about the same depth and somewhat larger than Eight Lake. During the summer, from July 22 to September 6, 1952, Imikpuk had a daily production of fixed carbon averaging 0.030 milligrams (as glucose) per square centimeter per day. Annual figures are not available, but it is likely that this production rate was maintained for only three or four months, and that during the rest of the year there was very little photosynthesis. If this rate were maintained for 120 days the annual productivity would be 3.6 milligrams per square centimeter. If the productivity of Eight Lake has been about the same for the past six thousand years as the present productivity of Imikpuk, an efficiency of utilization of gross production of about 75 per cent is indicated.

Some comparable figures for photosynthetic activity of Linsley Pond have been obtained by Riley (1940) during the months of September to June. They indicate a productivity of about 0.089 milligrams (as glucose) per square centimeter per day, which is not appreciably different from the rate in Imikpuk. The Imikpuk measurements, however, were made during the summer season, while the Linsley Pond measurements are for ten months of the year, omitting July and August. If those months were as productive as June and September, Riley's annual mean might be raised to about 0.11 milligrams per square centimeter per day, or 40 milligrams per square

centimeter for an entire year. If this rate held throughout C_2 and C_3 time, the diagenetic efficiency of Linsley Pond must have been about 80%. This is slightly more than the efficiency calculated for Eight Lake, which is only two meters deep as opposed to 15 meters for Linsley Pond. Deep lakes should, in general, have a higher efficiency than shallow ones. The settling seston is subject to decomposition in the epilimnion of a deep lake that is comparable to the decomposition in the entire water column in a shallow one. In addition a certain amount of decomposition may be expected in the hypolimnion, despite the possible inhibitory influence of the low hypolimnetic temperature and oxygen tension that prevail there.

The figures for the amount of material preserved in the mud enable us to make some calculations concerning the relative importance of the energy flow through the decomposing organisms in a lake community. If we accept the respiration values culled from the literature by Lindeman (1942), then 26% of the gross productivity of a lake is used by producers and consumers in respiration. The balance of 74% is preserved in the sediments or used by decomposing organisms such as bacteria and fungi. If this proportion holds for our lakes as well, then the percentage of the gross production that passes through the decomposing organisms is about 54% in Linsley Pond and about 49% in Eight Lake. This is somewhat higher than the figure of 24% which can be derived from the data of Odum (1957) from Silver Springs, Florida. Odum's estimate of bacterial energy flow depended on *in situ* measurements of bacterial activity in the mud. If bacterial activity in the periphyton is not, as he assumed in his calculations, equal to activity in the mud, but is higher, then his estimate is too low. We cannot, however, make any very great adjustments in the estimated energy flow through producers in Silver Springs without upsetting the community energy budget, nor does any general expectation that the role of decomposers in all ecosystems should be quantitatively similar constrain us to do so. We feel that quantitative analysis of the relative importance of decomposers, consumers, and storage or export will yield results of great importance to ecology, *i.a.*, to the problems of terrestrial and aquatic paludification, and we regret only that the accuracy of our estimate does not enable us to pursue the subject any further.

The figures for rate of inorganic sedimentation given in the third column of Table 5 call for little comment. Their principal importance is that they show that the rate of silting in arctic lakes is greater, in general, than it has been in temperate Linsley Pond since its early history, but that Eight Lake, as is apparent from every other line of evidence as well, forms an exception and has lower rate of deposition of mineral sediment than Linsley Pond since the beginning of *C-2* time.

The figures for *Bosmina* fragments indicate a much lower productivity in the Arctic than in Linsley Pond. The extremely low value for Eight Lake is to some extent a reflection of the fact that the lake had passed through its phase of high *Bosmina* productivity before the beginning of the time under consideration in these computations, but the concentration per cubic centimeter at the lower levels is only about 100 times as great. Even a *Bosmina* production of 75 instead of 0.75 per square centimeter per year would be a good deal below the lowest value computed for Linsley Pond. Unfortunately the reality of this difference must be slightly suspect, for the arctic *Bosmina* consisted of poorly preserved fragments instead of the half-carapaces so common in Linsley sediment.

With tendipedids, however, the story is different. Eight Lake appears to have had a productivity three times as great as that of Linsley Pond at its highest. The results cannot be regarded as conclusive because of the very great variation in the production, or at least the standing crop, of tendipedids in the temperate zone (Deevey 1941).

DISCUSSION

The principal characteristics of the arctic environment are its cold, with long severe winters and short cool summers, and the very marked seasonal distribution of insola-

tion. To a very considerable extent low precipitation is characteristic of the arctic regions as well.

The question that we had in our minds throughout this investigation is to what extent, if at all, these peculiar properties of the Arctic influence the workings of its lakes. We believe that we have found that the regional limnology of the Arctic is peculiar, but not always in the way that one would expect.

In the first place, the extreme cold of the far north does not seem to have a very great direct effect, except perhaps at the shore, upon life in the water. The lakes we have studied are not very large ones, and they attain summer temperatures of 12 or 13°C. This is no colder than the summer temperature of many deep lakes much farther south. For example, Lake Superior, at a latitude of about 48°, attains a maximum open water surface temperature of only about 10°C., although isolated bays and shallow water near shore may be somewhat warmer (Millar 1952). The well known thermal properties of water act to buffer aquatic organisms against the regional thermal environment, and the actual temperatures to which aquatic organisms are subjected are as much a function of lake size and shape as of latitude.

This is not to say that the length of the growing season is not affected by the shortness of the arctic summer; it is, but a short growing season is not restricted to the far north. In ephemeral lakes of the temperate and tropic zones the length of the growing season is limited by summer drought, and most aquatic organisms, at least of the smaller kinds, are adept opportunists, able to take advantage of favorable circumstances when they offer and to endure long resting phases of very low activity with little ill effect.

The seasonal distribution of insolation seems to influence mineralization. Although Eight Lake has a diagenetic efficiency somewhat less than that of Linsley Pond, the state of preservation of fossils in the sediment of the various lakes leads us to believe that the diagenetic efficiency of other Brooks Range lakes, particularly Chandler Lake, is very much greater. This is to be expected, for not only does the seston of a deep lake like Chandler have to fall a greater distance before it is preserved in the bottom mud, but a much greater reserve of dissolved oxygen is trapped under the winter ice to be available for oxidizing the organic component of the seston during the season of darkness.

The secondary characteristic of the arctic climate, low precipitation, has even less effect on life in the lakes. For most of the year the temperature remains below freezing and the light snowfall accumulates. Summer temperatures are so low that evaporation is not high and the frozen ground prevents subsurface run-off. As a result water is not scarce, despite low precipitation, and the arctic lakes do not show the striking seasonal variations in level so characteristic of lakes in other arid and semiarid lands.

Although the direct effect of the arctic environment on the biology of lakes does not seem to be pronounced, the effect on their physiography, and through it on all aspects of lake metabolism, is very great indeed. On the coastal plain the very existence of lakes, as well as their peculiar shape, their growth, and their ultimate disappearance, are due to the physiographic effects of the arctic climate. Even in the mountains, where the lakes owe their existence to past climatic phenomena that are not unique to high latitudes, the effect of climate on lake physiography is profound, not only in such minor things as the sculpturing of beaches but also in such important ones as the nature and amount of allochthonous sedimentation.

SUMMARY

1. Thaw lakes in northern Alaska occupy elliptical basins with a regular bottom, which appear to be in equilibrium with the environment, and irregular basins with pocked bottoms, which appear to be actively expanding and reducing the level of the landscape by about 15 meters.

2. Computations based on the shape of the active lake basins indicate that about 70% by volume of the upper 15 meters of the countryside consists of ice.

3. Active thaw lakes can be distinguished

from kettle lakes by the fineness of the bottom pitting. Quiescent thaw lakes can be distinguished from kettles by their smooth bottom contours.

4. The water of the Alaskan lakes freezes to a depth of almost two meters in winter and warms to about 13°C in summer. The lakes are unstratified during the summer months.

5. Although prevailing wind velocities are high the work of the wind in warming Chandler Lake, which is 21 meters deep, is only 175 cal/cm^2 of lake surface. The annual heat budget is about 28,000 cal/cm^2, of which only about 6,000 cal is wind-distributed heat.

6. There is a net flow of heat from the water to the earth in the case of lakes too deep to freeze solid in winter.

7. The total dissolved solids of the lakes investigated ranged from 35 to 159 ppm. At the seacoast Na^+ and Cl^- were the dominant ions. Elsewhere Ca^{++} and HCO_3^- were more important.

8. Silica was not detected in field tests, but up to 1.9 ppm of silica was found in samples that had been stored in pyrex bottles for several months.

9. The shore community is poorly developed or lacking in most arctic Alaskan lakes.

10. Standing crops of benthic organisms are low but not markedly so. Benthos ranged up to 89.4 kg/ha.

11. Most of the arctic lakes receive a very large contribution of allochthonous sediment.

12. *Dryadotanytarsus* is found throughout the sedimentary column of Eight Lake in Alaska and presumably lives there today.

13. In all the lakes investigated *Pediastrum boryanum* increases in abundance from the bottom to the top of the sedimentary column. This increase appears to be associated with shoaling.

14. Eight Lake, which has a good fossil record, appears to have passed from an early eutrophic stage with high productivity of *Bosmina* and tendipedids to a later dystrophic stage with low animal productivity and high productivity of mosses. This change is attributed to exhaustion of the available base supply in the watershed.

15. Using a radiocarbon-dated pollen chronology, estimates have been made of the net community productivity of the Alaskan lakes. It appears to have averaged less than 2 mg of organic matter/cm^2/yr during the past 6,000 years, as compared to 8 mg/cm^2/yr for Linsley Pond, Connecticut, during a comparable period of time, and 7 and 4 mg/cm^2/yr during earlier times.

16. On the basis of several more or less reasonable assumptions the efficiency of utilization of gross production is calculated to be 80% for Linsley Pond, Connecticut, and 75% for Eight Lake, Alaska. It is probably somewhat higher for the other Alaskan lakes.

17. On the basis of the same assumptions plus the respiration percentages of Lindeman, it is calculated that about 50-55% of the energy fixed by producing organisms passes through the decomposer level in a lake food-chain.

18. Less than 10 *Bosmina* fragments have been preserved per square centimeter per year during the past 6,000 years in the Alaskan lakes as compared to 400, 700, and 4,000 per year for various stages in the development of Linsley Pond. Corresponding figures for tendipedid fragments are less than 1, 1, and 7 for the Alaskan lakes and 0.4, 0.7, and 2.2 for Linsley Pond.

19. The arctic environment appears to influence lakes principally through physiographic processes affecting origin, sedimentation, and drainage.

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Measurements of Primary Production on Southampton Island in the Canadian Arctic[1]

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ABSTRACT

Primary production in two lakes of contrasting morphometry in the Canadian Arctic was estimated independently from the differences in oxygen, pH, and carbon^{14} uptake between light and dark bottles. The estimates were in general agreement. Together with production estimates from two other high latitude lakes reported in the literature the data show that the morphometry of the lake basins exerts a considerable control over rate of production, with the shallower lakes having a higher intensity of production (g C/m^3/day) than the deeper lakes. The available data also suggest strongly that the rate of production is generally low in the Arctic, and that the amount of production accomplished by the more productive lakes is roughly the same order of magnitude as that of the least productive temperate lakes reported in the literature.

Measurements of primary production were made on two lakes of contrasting morphometry (Table 1) in the Canadian Arctic during the brief period 10 through 26 August 1957. Lake S-1 located directly behind the school at the Settlement of Coral Harbour is representative of the many shallow lakes and ponds in the tundra. It has an estimated area of only a couple thousand square meters and a maximum depth of less than a meter. It occupies a depression in Precambrian gneisses, but because the island is generally covered with calcareous drift, even in these regions of crystalline rocks the methyl orange alkalinity of the water is moderately high.

Although Lake S-1 is located moderately close to a number of Eskimo dwellings, there is little opportunity for enrichment of the water by natural drainage because the lake is at a higher elevation than the dwellings. The school and the two white dwellings close to the lake do not contribute any sewage. The standing crop of phytoplankton in this lake was not noticeably greater than in more distant shallow lakes of the region.

Lake S-7 is a much larger lake about 6 km long by 0.7 km wide, with a surface area of roughly 3.5 km^2 (as measured by planimeter from work sheets of the Canadian Department of Mines and Technical Surveys) and a maximum depth of at least 10 m. Judging by the distribution of color in the lake as seen from the air, the absolute maximum depth is not much greater than this. The mean depth of the lake was estimated to be about 6 m. The lake is located along the northeast side of a high ridge ("The Points"), which is variously interpreted as being an esker, an interlobate moraine (Bird 1953), or a ridge of the Ordovician and Silurian limestones which comprise the bedrock of the southwestern two-thirds of the island. It is interesting that the methyl orange alkalinity of this large lake

[1] Contribution No. 646, Department of Zoology, Indiana University. The authors were privileged to participate in a brief expedition to Southampton Island, organized and sponsored by the Indiana Gear Works of Indianapolis, Mr. John Buehler, President. The Indiana Gear Works also arranged for Dr. J. H. Ryther of the Woods Hole Oceanographic Institution to furnish the necessary field equipment for the C^{14} studies and to make the C^{14} counts at Woods Hole. The authors wish to acknowledge their gratitude to all persons concerned.

[2] The results reported originally by Comita and Edmondson are in error. Based on recalculations by Comita and at his request the pertinent two sentences on page 8 are here amended to read: "During the summer of 1952 the production of oxygen varied from 0.025 to 0.359 mg/L/day (mean 0.154). The corresponding rates per square centimeter of lake surface varied from 0.005 to to 0.074 mg/cm^2/day (mean 0.032)." On page 9 the efficiency for Imikpuk should read 0.035% instead of 0.085%.

TABLE 1. *Basic data for lakes S-1 and S-7 on Southampton Island*

Lake	Location	Elevation m	Approx. area ha	Depth — m		Mean light transmission %	Calc. depth 1% level m	MO alkalinity as ppm $CaCO_3$	Dissolved color ppm
				Known max.	Est. mean				
S-1	64° 8′ N, 83° 10′ W	6	0.2	0.7	0.6	30	3.6	79	33
S-7	63° 36′ N, 85° 4′ W	98	350	10	6	78	18	55	<10

located in a strongly calcareous region is only two-thirds as great as that of the smaller lake in the crystalline region.

Except for this ridge the relief of the areas studied is rather small, and both lakes are openly exposed to the strong winds that blow from the northern sector most of the time. Because of the wind even the deeper lake circulates continuously during the short ice-free period, and cooling can occur very rapidly. Both lakes would have to be designated as third-order temperate or dimictic lakes in the terminology of Hutchinson and Löffler (1956) and Hutchinson (1957).

The climatic regime at Southampton Island is much more severe than might be inferred from the latitude. In the Hudson Bay Region the isotherms are depressed strongly to the south, and as a result the northward limit of trees is located several hundred miles south of Southampton Island in the general vicinity of Churchill. The only "trees" on the island are low scrubby or even prostrate willows, seldom as high as 1 m.

METHODS

Independent estimates of primary production were made from the differences in pH, dissolved oxygen, and C^{14} uptake that developed between duplicate samples of water in light and dark bottles after having been suspended at their depth of origin for appropriate periods of time. Ryther (1956) has already pointed out that of these three methods C^{14} uptake is most sensitive, and that pH change as measured by the ordinary pH meter is least sensitive. The rate of production in Lake S-1 was sufficiently high so that all three methods could be used, whereas in Lake S-7 only the radiocarbon method was used. The literature regarding these methods of measuring photosynthesis has recently been reviewed by Lund and Talling (1957).

Pyrex bottles of 125-ml capacity with pointed glass stoppers were filled with water collected by means of an ordinary Kemmerer water sampler. Hence, although the calculated photosynthetic rates are undoubtedly somewhat low from inactivation by the metal water bottle, their consistency with previously reported estimates of production indicates that the errors are not excessive and do not invalidate the conclusions of this paper.

Oxygen method (Gaarder and Gran 1927). Dissolved oxygen was measured by the unmodified Winkler procedure. The titration results (N/80 $Na_2S_2O_3$ with 100-ml samples) were corrected for volume of reagents added and volume of oxygen added with the reagents according to the procedure described by Ohle (1953).

pH method (Verduin 1956). pH was measured with a Beckman Model N pH meter, which seemed to function very satisfactorily in the Arctic summer. By determining the pH of a 100-ml sample of water after successive additions of small amounts of N/44 HCl, a titration curve was established for each lake, from which any change in pH could be related to the quantity of acid (hydrogen ions) necessary to produce the change. This in turn was translated into the quantity of CO_2 (as H_2CO_3) involved in the overall metabolism of the water sample.

C^{14} method (Steemann Nielsen 1952, and Steemann Nielsen and Aabye Jensen 1957). Each bottle of a pair was inoculated with 0.5 ml of a $Na_2C^{14}O_3$ solution having an activity of 3.3×10^6 counts/min./ml. After a suitable period of exposure each sample was filtered with suction through a Type HA Millipore membrane having an effective filtering area 22 mm in diameter. For Lake

S-7 the entire 125 ml could be filtered in a few minutes. For Lake S-1 the plankton content was so high that only a 50-ml sample could be filtered in a reasonable period of time. Each filter was washed with 10 ml of 0.001 N HCl and stored in a small glassine envelope in an opaque desiccator until the activity could be determined.

To translate the C^{14} counts into total uptake of carbon by photosynthesis, the quantity of available carbon in the water must be known. For each of the four series of experiments this quantity was calculated from the initial pH and the methyl orange alkalinity by means of the equations presented by Moore (1939). From the fact that the water in both lakes is strongly influenced by limestone and calcareous drift and the fact that the titration curves exhibit the double inflection characteristic of the $CaCO_3$-$Ca(HCO_3)_2$-H_2CO_3 system, it is reasonable to assume, in the absence of a complete mineral analysis, that the carbon dioxide complex was the chief determinant of the methyl orange alkalinity.

Other properties. Water temperatures were measured with a Whitney thermistor reading directly to 0.1° C. Relative intensities of visible light at various depths in the water were measured with a light meter also assembled by Whitney containing a Weston photronic cell. The relative light values plotted on semi-log paper as percentages of surface light enabled the estimation of the mean transmission of light by the water and the estimation of the depth of the 1% level. Intensity of daylight in foot-candles was measured with a General Electric DW-68 exposure meter, employing the appropriate incident light mask. An attempt was also made to measure radiation directly as g-cal/cm²/min. by means of a General Electric infrared meter Model 8DW69Y1, but this was not sensitive enough for the levels of radiation encountered.

RESULTS

Table 2 lists the estimates of primary production for each experimental series, unadjusted for the duration of the experiment. To obtain production per day the results for Series II should be halved, and those for Series IV should be increased by about 40%. The data used in calculating primary production by the C^{14} method are given in Table 3. Of the various estimates of primary production in Lake S-1 those based on the C^{14} method are of greatest significance, in that this method is the most sensitive of the three employed. Ryther (1956) believes that calculations based on C^{14} uptake approximate net photosynthesis, and apparently this idea is now being accepted by other persons using the C^{14} method.

TABLE 2. *Carbon fixation in lakes S-1 and S-7, Southampton Island, unadjusted for duration of experiment*

Lake and Series	Date and time 1957, C. D. T.	Duration hr	Max. water temp. °C	Depth m	mg C/m³			mg C/m²		
					C^{14}	O_2	pH	C^{14}	O_2	pH
S-1 I	0520–1945 Aug. 13	14¼	10.3	0	*	90	58	58	52	30
				0.6	96	81	41			
II	1130 Aug. 14–1130 Aug. 16	48	11.6	0	79	90	89	46	80	48
				0.6	75	177	72			
S-7 III	0930 Aug. 18–1000 Aug. 19	24½	8.2	0	*			13		
				1	1.8					
				5	1.2					
				9	1.5					
IV	1300 Aug. 19–0900 Aug. 20	20	7.0	0	0.5			10		
				1	1.5					
				3	1.9					
				5	0.7					
				7	0.5					

* Samples inadvertently lost.

Table 3 shows that in Lake S-7 the dark fixation of carbon was constant at all depths in both series, which is to be expected since the length of exposure was approximately the same in the two series and the lake was turning over vigorously. In Lake S-1 the amount of dark fixation would be expected to be higher in Series II than in Series I because of the longer duration of the former. This is true for the bottom sample but not the surface sample of Series II. Dark fixation increased from 1.1% in the 14-hour exposure (Series I) to 2.9% in the 48-hour exposure (Series II), which points out as others have done (Steemann Nielsen and Aabye Jensen 1957) the advisability of using short exposure times in C^{14} experiments.

The results indicate that the shallow lake

TABLE 3. *Data used in calculating primary production by C^{14} method*

Lake and Series		Initial pH	MO alkalinity ppm $CaCO_3$	Total inorg. C* mg/L	Depth m	C^{14} counts/min. Light	Dark	Net, adjusted for 6% isotope effect
S-1	I	8.16	78.4	9.69	0.6	15,644	171	16,401
	II	8.36	79.6	9.73	0	12,780	192	13,343
					0.6	12,350	361	12,708
S-7	III	8.27	54.5	6.69	1	447	39	432
					5	317	49	284
					9	361	21	360
	IV	8.19	55.7	6.88	0	146	39	113
					1	371	39	352
					3	451	30	446
					5	191	24	177
					7	143	32	118

* Calculated from the pH and methyl-orange alkalinity by means of Moore's (1939) equations.

(S-1) has a production intensity (mg C/m³/day) roughly 60 times greater than the deep lake (S-7). This could have been roughly anticipated in advance on the basis of the optical properties of the water and the amount of plankton visible to the eye. The production per square meter, however, is only about four or five times as great. Ruttner (1952) has already pointed out that rates of assimilation differ much more from one lake to another when related to unit volume of water of the trophogenic zone than to unit surface area of the lake. This same matter is presented in greater detail by Vollenweider (1956).

The estimates of primary production in Lake S-1 calculated from oxygen and pH measurements are less valuable than the C^{14} estimates, although of the same general magnitude. The calculations based on the pH determinations are smaller than those based on oxygen, which may be in part a result of the low temperatures at which the measurements were made. Since the pH differences involved amounted to only 0.08 to 0.17 pH unit, the pH meter was being operated near its limit of sensitivity.

Assuming the methyl orange alkalinity remained constant in the bottles of Series I and II during the exposure periods, the free CO_2 was calculated for each initial and final pH from Moore's (1939) equation, and for the difference between the bottles of each pair the carbon uptake was calculated. These results are even smaller than those determined from the titration curves, being only 73% as high for Series I and 83% for Series II. Hence, it appears that the pH method is of limited usefulness in estimating photosynthesis in situations such as these.

The production estimates based on oxygen changes are probably more reliable, except for the bottom sample in Series II which is obviously too high, since in the other four pairs of values production at the bottom is somewhat less than at the surface. Except for this sample, differences in oxygen content between light and dark bottles amounted to 0.27 to 0.30 ppm, and hence the production estimates in Table 2 should be within about 20% of their true values.

In Lake S-1 with a light transmission averaging only 30% per meter, production at 0.6 m was less than at the surface even on bright days, whereas in Lake S-7 with a mean transmission of 78% per meter, production in Series IV during a generally overcast day was greatest a short distance below the surface. These somewhat anomalous results are difficult to explain from the data available.

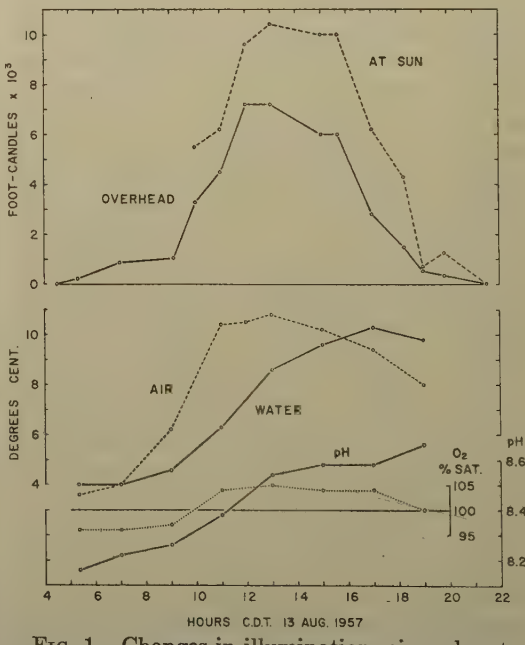

FIG. 1. Changes in illumination, air and water temperature, pH and oxygen saturation at Lake S-1 on 13 Aug. 1957.

Figure 1 shows the course of several meterological and limnological factors at Lake S-1 during the daylight hours of 13 August. The sky was overcast until about 0900, then cleared appreciably, with 30 to 60% cover of thin cirro-stratus clouds for the rest of the day. There was a moderately strong to strong wind throughout the day.

The air temperature increased rapidly, generally following the curve for illumination. The water temperature lagged behind appreciably, even with the wind. The curve for per cent saturation of oxygen follows the curves for air temperature and illumination more closely than the curve for water temperature, indicating that the slight supersaturation from 1100 to 1700 hours was brought about at least in part by photosynthetic activity. This idea is substantiated by the rather marked increase in pH during the day. The oxygen liberated as a result of photosynthesis was quite rapidly released to the air from the strongly agitated water, but the CO_2 utilized in photosynthesis could not be replenished nearly so rapidly from the atmosphere. As a result the pH was markedly affected. The pH at 1900 hours would not be expected to increase further because of the greatly reduced light values, and hence this value may be in error.

The rate of production calculated from the pH of 8.16 at 0520 hours and 8.58 at 1700 hours is 178 mg C/m³, which is about twice as high as any of the other estimates for Series I. The difference may possibly indicate the relative importance of the benthic algae in the overall primary production of this shallow lake.

The temperature data for Lake S-7 are interesting in that they show how rapidly even a large Arctic lake can cool off under the influence of strong cold winds. The water of the entire lake cooled from 10.2° at 1230 hours on 15 August to 9.2° at 1400 hours on 17 August, to 8.2° at 0900 hours on 18 August, and to 6.9° at 1000 hours on 19 August.

DISCUSSION

With its great sensitivity the C^{14} method of measuring photosynthesis is certain to become widely employed in limnology, as it already is in oceanography. To date, however, there are very few investigations published. Lund and Talling (1957) list just four, of which the one by Nygaard (1955) is the earliest.

Table 4. *Rates of primary production in four subarctic and arctic lakes arranged in order of increasing depth*

Lake	Location	Area ha	Depth m		mg C/m³/day	mg C/m²/day	Method
			Max.	Mean			
S-1	64° 8′ N, 83° 10′ W	0.2	1	ca.0.6	90	50	C^{14}
Imikpuk[1]	71° 17′ N, 156° 40′ W	61	2.1	2.1	58	120	O_2
Bare[2]	57° 11′ N, 154° 19 W	49	7.5	7.5	25	100	O_2
S-7	63° 36′ N, 85° 4′ W	ca.350	10	ca.6	1.5	9	C^{14}

[1] Mean of period 22 July to 6 September 1952.
[2] Pre-fertilization in June-July, 1950–53.

Of more importance to the present study is the rate of production in the Arctic. Welch (1935) suggested that there might be a greater standing crop of phytoplankton in polar fresh waters than toward the tropics, implying that the rates of production varied correspondingly. Few studies on primary production in the Arctic are available for comparison with the present study, and none that have employed C^{14}.

Comita and Edmondson (1953)[2] reported a summary of production estimates based on the oxygen procedure for Imikpuk Lake near Pt. Barrow, Alaska. Production varied from 9 to 135 mg C/m³/day (mean 58), and from 19 to 278 mg C/m²/day (mean 120). These results are based on an RQ of 1. They would be 20% lower for an RQ of 1.25, as Ryther (1956) recommends. Hence, Imikpuk has about the same rate of production per m³ as Lake S-1, but because of being deeper it shows a correspondingly higher rate of production per m². Both lakes, however, are much more productive than Lake S-7.

Bare Lake on Kodiak Island, Alaska, has been studied by the oxygen method (Nelson and Edmondson 1955). Before fertilization gross primary production (RQ = 1) aver-

aged about 20 or 30 mg C/m³/day. In response to fertilization production increased to 150 and even to more than 200 mg C/m³/day, but in all instances the rates of production rapidly declined after the peak response, leaving no residual effect detectable the next year. Since the mean depth of the lake is 4 m, the base level of production for the lake as a whole averages about 80 to 120 mg C/m²/day, with correspondingly greater values under the influence of fertilization. Thus, Bare Lake exhibits the same general level of production as Imikpuk and Lake S-1.

The estimates of production for these four lakes in the North American Arctic and Subarctic are summarized in Table 4. As expected, the rate of production per unit volume of water is much greater in the shallow lakes than in the deeper lakes. In the shallow lakes not only the water but the entire substrate as well can be actively involved in photosynthesis, and any mineralization products can become immediately reincorporated into the metabolic cycle. The morphometric control of production in the Arctic seems to be as important as in temperature latitudes of the northern hemisphere.

Imikpuk Lake was free of ice for 65 days. If the mean rate of gross production listed in Table 4 prevailed throughout this period, a total of 7.8 g of carbon or about 20 g of glucose was fixed during this period. Assuming that relatively little additional production occurred under the ice, this annual production is much less than any of those listed by Vollenweider (1956) for European lakes and adjacent marine areas. Even if this daily rate of production had been maintained over the entire year, the total production accomplished would only have equalled that of the least productive European lakes reported.

At the other extreme, even if Lake S-7 had maintained its rate of production throughout the year, the result would have been much less than that in any lake listed by Vollenweider, or of Lunzer Untersee as listed by Steemann Nielsen and Aabye Jensen (1957). It would also have been much less than the net annual phytoplankton production for the Sargasso Sea (50 g C/m²/yr, as listed by Riley 1957), a region notoriously low in production.

Thus, our present information indicates that the rate of primary production in arctic fresh waters instead of being categorically high is generally rather low. It is markedly influenced by the morphometry of the particular basins, with the rates in the shallow, more productive waters approaching those of some of the less productive temperate lakes. The total amount of net production accomplished per year is low in comparison with temperate latitudes.

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The Seasonal Growth and Succession of Plankton Algae in the White Nile

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ABSTRACT

A description is given of the seasonal growth and succession, over five years, of planktonic algae in a region of the White Nile affected by a reservoir. Dense populations develop during the period of water storage, and are dominated by the diatom *Melosira granulata* and the bluegreen alga *Anabaena flos aquae* var. *intermedia* f. *spiroides*. The sequence of their development is related to their abundance in the river water entering the reservoir basin. Reactions of algal development upon water characteristics include a considerable increase in pH and depletion of nitrate, phosphate, and probably silicon concentrations. Deficiency of inorganic nitrogen probably limits the maximum densities of *Melosira*. Maximum algal densities were in the range 20 ± 8 mm^3 cell volume (or approximately mg dry weight) per L, and were associated with high rates of photosynthetic production, estimated in 1953 as approximately 2.2 g carbon/m^2/day. The variation of photosynthetic rates with depth and population density is described for the decline of the 1953 population maximum.

INTRODUCTION

The seasonal growth of plankton algae in tropical freshwaters is a largely unexplored subject. Almost all detailed quantitative knowledge of plankton periodicity is derived from temperate regions, where the timing of the annual cycle is usually influenced by the pronounced winter minimum in solar radiation. This seasonal check to phytoplankton growth is absent in the tropics, and it has been held that conditions in a large tropical lake "allow the phytoplankton to grow continuously and to a density limited only by the availability of some essential nutrient salt" (Beauchamp 1952). At present there appears to be no seasonal study sufficiently detailed to test this statement. In particular, it is not clear to what extent the nutrient limitations may operate discontinously in time, so as to delimit temporary maxima or "pulses" of phytoplankton growth comparable in form to the classic spring maxima of many temperate waters. Fish (1957) has shown that such brief maxima may develop in response to a seasonal breakdown of stratification in Lake Victoria. Their origin under other circumstances in tropical waters is described in the present paper.

The evidence is derived from a quantitative study of phytoplankton growth and decline in the White Nile near Khartoum. Here the yearly closure of a dam creates a temporary "river-lake" in which dense populations of phyto- and zoo-plankton develop. Between 1951 and 1956 this development has been followed quantitatively in both space (along the river) and time. Some spatial aspects have been described in detail by Brook and Rzóska (1954) from observations in December 1951, and a summary of the main features of seasonal succession between 1951 and 1953 is given by Rzóska, Brook, and Prowse (1955). The latter evidence shows that although high densities of phytoplankton are only realized during the period of water storage, the numbers of several species become limited, or decline, before the end of that period.

In this paper such cycles of growth are described from the full five-year period for which estimates of algal densities are available. For the last two years a comparison is made between algal development and and certain physical and chemical factors of the environment, in an attempt to identify the factors limiting the algal maxima. Particular attention is given to the reaction of algal growth upon water characteristics,

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a subject which is also illustrated from longitudinal surveys along the river. Algal maxima are assessed in terms of both morphological units and—for wider comparison—by the amounts of materials estimated to be incorporated in the crops. Changes in the magnitude of primary productivity, measured as the rate of photosynthetic production under unit area, were followed during one population maximum. Estimates of photosynthetic production, and its control, on other occasions are described by Talling (1957c).

We wish to express our indebtedness to Dr. A. J. Brook for making available his unpublished data, to Mr. F. J. H. Mackereth for chemical analyses of algal cells, and to the Egyptian Irrigation Department in Khartoum for hydrological data. This work forms part of the studies on Nile biology carried out by the Hydrobiological Research Unit of the University College (now University) of Khartoum. To its stimulating leadership by Dr. J. Rzóska, and his continuous help and assistance when on the river, we owe the greatest debt of gratitude. Finally the paper has benefitted from helpful comments by Dr. J. W. G. Lund.

METHODS

Seasonal changes were followed by means of water-samples collected from one locality (Gordon's Tree) some 40 km below the dam at Gebel Aulia (see map in Brook and Rzóska 1954, Fig. 1), above which water storage occurs. Longitudinal surveys along the river, described by Brook and Rzóska (1954) and on pp. 224–6, show that the density and composition of the plankton at this sampling station are generally similar to that present in the reservoir immediately above the dam. Consequently the seasonal changes recorded are likely to be a close "reflection of the annual plankton cycle in the basin itself" (Rzóska *et al.*, 1955, p. 333). Direct knowledge of conditions in the basin was obtained from series of samples taken longitudinally up the river in December 1953, June, October and December 1954, and October 1955. Certain gaps in the sampling record (see Fig. 2) were due to our absence from Khartoum, but chiefly occurred when the reservoir was discharged and the phytoplankton growth small.

On all occasions samples of surface water were taken, and during 1951–3 samples from the middle and bottom of the water-column as well collected at a considerable distance from the bank. Plankton counts from the various depths were then averaged, as indicated by Rzóska *et al.* (1955). For 1954–6 all the estimations given here refer to surface samples, as the previous observations had shown that there was usually little or no indication of marked stratification of plankton at the Gordon's Tree station (cf. also Brook and Rzóska 1954, Table 1). In the deeper areas of the reservoir basin diurnal changes of thermal stratification may cause a surface accumulation of bluegreen algae in the afternoon (Talling 1957c), but samples obtained under such circumstances are not considered in the present account. The stratification of algae recorded by Brook and Rzóska (1954) is not large enough to affect seriously the reliability of population census based on surface samples. A similar conclusion was reached from a comparison of surface and bottom samples collected along the basin in October 1954. These samples also showed little stratification in water characteristics other than temperature, dissolved oxygen, and pH, which were subject to a pronounced diurnal stratification near the dam (Talling 1957c).

The samples from the middle and bottom layers were collected using a Friedinger or Ruttner sampler. Counts of phytoplankton were made with a Naumann cell during 1951–2 (Brook and Rzóska 1954, p. 103), with a Sedgwick-Rafter cell during 1952–5, and using an inverted microscope and iodine sedimentation method (Utermöhl 1931, Lund 1949) during 1955–6. In the 1952–5 estimations the volumes of water involved in the counts were about 0.05–0.10 ml (as areal percentages of the total volume, 1 ml, in the counting cell). With the inverted microscope, the volumes used were sufficient to yield 50–100 individuals of the principal algae. Counts of algae during 1951–2 were made by Dr. A. J. Brook, who has kindly

placed unpublished data at our disposal. Estimations of physical and chemical water characteristics were made by the methods described by Talling (1957e). The procedure involved in field experiments on photosynthesis has also been described elsewhere (Talling 1957c). Samples of surface water were used in exposures of 1–3 hours.

The dry weight and chemical constitution of algal material were obtained using net catches, collected on 30 October 1955 (*Melosira*) and 12 October 1955 (*Anabaena*). Total organic nitrogen was determined by a micro-Kjeldahl method, total phosphorus by the method of Mackereth (1953), and silicon by the ammonium molybdate method after solution with sodium hydroxide. Sulphur was estimated after oxidation to sulphate, using ion exchange resins. We are greatly indebted to Mr. F. J. H. Mackereth for these analyses.

THE HYDROLOGICAL BACKGROUND

The magnitude and timing of the chief hydrological events, the storage and release of water in the reservoir basin, vary only slightly in successive years. An outline of these changes is given below; Hurst (1950) gives a detailed account covering earlier years. The main closure of the dam and filling of the basin occurs between 14 July and 21 August, the exact period varying in different years (Fig. 2). A secondary filling occurs after 1 September, and the high level then reached persists until February–April, after which the storage water is progressively released. The timing of the release also varies slightly in different years. Falling water levels and true river conditions prevail until the next filling after July.

The most obvious and probable overriding effect of water storage is the increased time made available for the growth of plankton algae in the reservoir basin. This additional time can be estimated from a knowledge of the rates of water discharge at the dam, and the storage capacity of the basin estimated from water levels according to Hurst (1950). An estimate for the period of high water level, calculated by dividing the estimated water storage by the discharge, is approximately 40–70 days. Loss of water by evaporation is neglected here, but involves only a minor correction. The application of a similar measure to the problems of plankton development in small water bodies has been discussed by Brook and Woodward (1956).

An additional but natural damming affects the lowest region of the White Nile (including the sampling station at Gordon's Tree) in each year, usually during July and August. At this time high flood water in the Blue Nile at its junction with the White Nile produces a secondary damming of the latter (see Hurst 1950), into which some brown flood water from the Blue Nile penetrates. Samples collected at Gordon's Tree at this time require special interpretation (see Fig. 3 and p. 230).

LONGITUDINAL SUCCESSION ALONG THE RIVER

Knowledge of the development of phytoplankton with distance along a slowly moving water mass, as is present in the reservoir basin, can clearly provide evidence on development in time. From this viewpoint four longitudinal surveys of the basin are considered below, beginning with the survey in 1951 by Brook and Rzóska (1954). The results are compared later with the temporal changes observed at the single station below the reservoir.

Sampling in several seasons has shown that the diatom *Melosira granulata* (Ehr.) Ralfs, with its narrow "variety *angustissima*" (discussed below) is generally the predominant plankton alga in the river above the main reservoir region (Brook and Rzóska 1954, Table 1; Prowse 1954). It is present there in comparatively low densities, often below 100 cells per ml, which have not been estimated with accuracy. In December 1951 these densities were found to increase between 410 and 80 km from Khartoum (Stations 15 to 4).[3] At this point the increase was halted, and there were no very significant changes in the lower stations near the dam (nos. 4 to 1). Also present at the lower stations were large densities of bluegreen algae, dominated by

[3] The scale of Brook and Rzóska (1954, Fig. 2) is in miles and not km as stated.

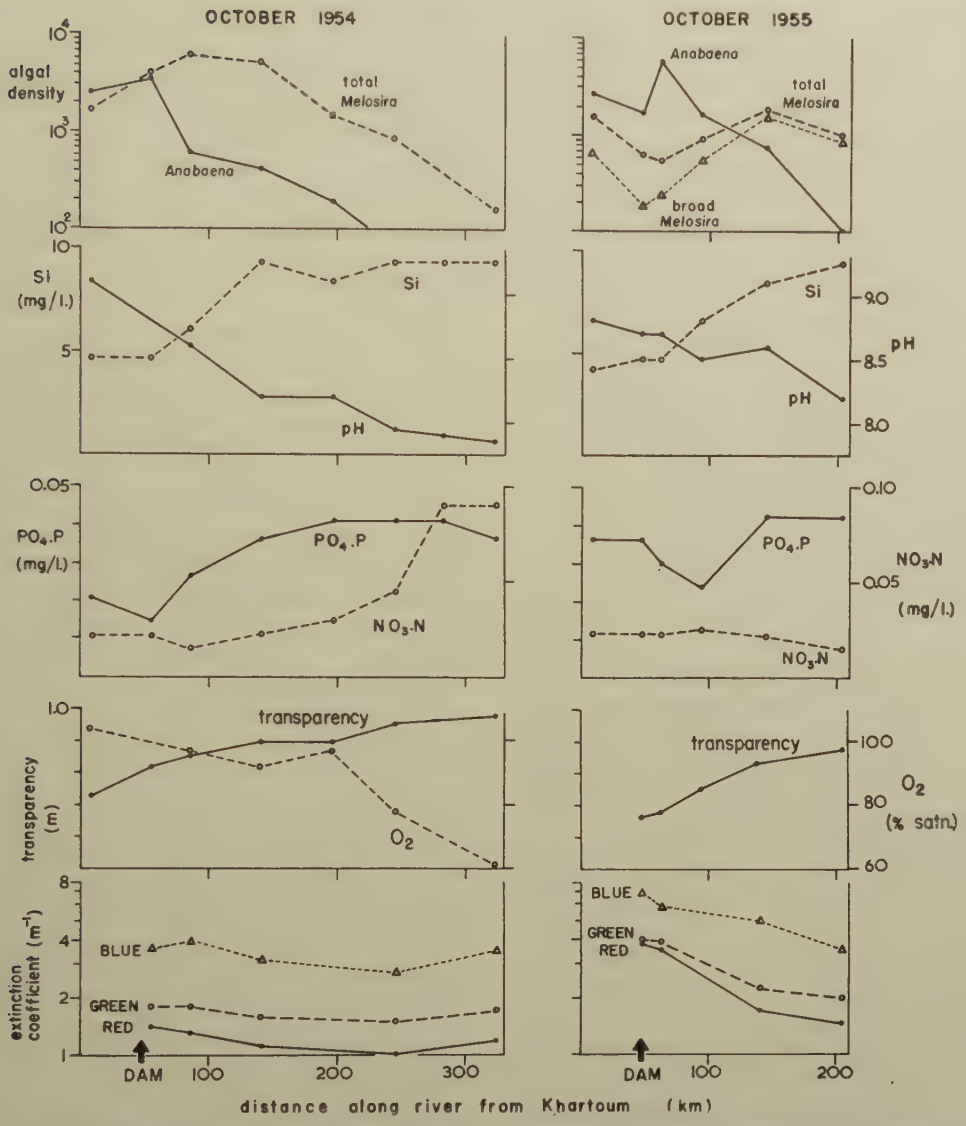

FIG. 1. The longitudinal variation along the river, during 3–7 October 1954 and 10-11 October 1955, of (a) algal densities, in cells per ml (*Melosira*) or coil-turns per ml (*Anabaena* * *spiroides*) on a logarithmic scale; (b) pH and dissolved silicon; (c) phosphate phosphorus and nitrate nitrogen; (d) transparency, and dissolved oxygen (% saturation); (e) vertical extinction coefficients for red, green, and blue light shown on a logarithmic scale.

Anabaena flos aquae Born. et Flah. var. *intermedia* f. *spiroides* Woron. (hereafter shortened to *Anabaena* **spiroides*). These algae were present in extremely low, and usually indeterminable, densities at the upper stations. Probably due to this handicap, their observed increase to high densities near the dam occurred later (*i.e.*, further downstream) than was the case for *Melosira*. Besides the dominant *Anabaena* **spiroides*, species of *Anabaenopsis* [*A. cunningtonii* R. Taylor and *A. tanganyikae* (G.S. West) Wolosz. et Miller], *Oscillatoria* [*O. geminata* (Menegh.) Gom. and *O. planktonica* Wolosz.], and *Lyngbya limnetica* Lemm. were present near the dam. A much less detailed survey in the same month of 1953 suggested a situation similar in essentials, although the

only significant bluegreen algae accompanying the *Anabaena *spiroides* near the dam were *Lyngbya limnetica* and *Anabaenopsis*.

Further longitudinal surveys were made during another season, October, in 1954 and 1955. The results (Fig. 1) differ from the December observations in that the only algae found in any numbers were *Melosira granulata* and its narrow "variety" (discussed below) and *Anabaena *spiroides*. The *Melosira* was again the most abundant alga upstream, and reached densities approaching the maximum levels much earlier (*i.e.*, further upstream) than did the *Anabaena*. In the 1955 series many cells of the *Melosira* population appeared unhealthy, and the percentage of dead cells increased downstream towards the dam. An accompanying increase occurred in the percentage of narrow elongated cells, distinguished as the variety *angustissima*, at the expense of the broader cells of the species whose numbers actually decreased towards the dam (Fig. 1). In these and other observations the distinction between the species and variety was not sharp but often obscured by numerous intermediates. Consequently the two forms—at least as observed here—may not be genetically distinct, but separated only by the size diminution characteristic of diatom growth. They are hereafter referred to as "broad" and "narrow" forms of the species.

Several effects of algal development upon water characteristics were indicated in the longitudinal surveys; the evidence is given in Figure 1 and in Brook and Rzóska (1954). The latter describe an increase in turbidity, dissolved oxygen, and pH near the dam, the changes in oxygen and pH being connected with increased photosynthetic activity. Similar changes are evident in Figure 1. The relation with turbidity may be complicated or obscured by the distribution of other suspended material (p. 224, and Brook and Rzóska 1954, p. 103). In the series of December 1953 and October 1954 there was a good correlation between phytoplankton density (particularly of *Anabaena *spiroides*) and decrease in inorganic phosphate. In each of the two October series a pronounced fall in silicon is suggested; a decline in nitrate nitrogen in October 1954, and its low levels in October 1955, may also be noted. These features are considered later, with other evidence, in a quantitative discussion of the reaction of algal growth upon water characteristics.

SEASONAL CYCLES OF ALGAL NUMBERS

(a) *Melosira granulata*

Changes in the density of *Melosira granulata* at Gordon's Tree are shown in Figure 2 for five successive seasons of growth. The figure enables the variations to be compared with those of other species, and with the hydrological cycles of filling and emptying the reservoir basin. The relative importance of *Melosira* in the total algal crop is also assessed in terms of cell volume. Counts of total *Melosira* cells and of the broad cells are recorded separately, so that the difference between them measures the numbers of narrow and elongated cells ("var. *angustissima*").

The main annual increase in *Melosira* usually takes place in the period during, and immediately following, the filling of the reservoir basin. This increase is rapid in all years represented by sufficient evidence (*i.e.*, 1951-5), although the observations may be affected at certain times by flood water from the Blue Nile (p. 224). Nevertheless, it is clear that the *Melosira* populations rapidly attain densities approaching, or in some cases constituting, the yearly maxima. Some part of the increase may be due to the resuspension of living cells which had previously sedimented onto the mud surface. Such resuspension at times of increased water turbulence is important for the ecology of other *Melosira* spp. in various English lakes (Lund 1954b, 1955a) and Lake Victoria (Fish 1957, Talling 1957d). Direct evidence for the present reservoir basin is lacking, but here turbulence is not reduced by long periods of thermal stratification (Talling 1957c), and large areas of mud are exposed to desiccation when the water level is low.

The later behaviour of the populations varies considerably in the five growth seasons. In only one (1953–4) is there a smooth increase to a maximum density followed by

regular decline. During 1954–5 the later part of the increase, in September, is interrupted by a temporary decline, and a similarly placed but more pronounced interruption is present in 1955–6. In 1951–2 and 1952–3 the primary increase is not halted until November, and the succeeding decline persists longer before a secondary increase appears. Variability between successive years is also characteristic of the timing of the final decline.

The proportion of narrow and elongated cells in the total *Melosira* population changes significantly according to the phases of population growth. It is generally small during periods of population increase, becoming larger during population decline. These facts, and the longitudinal succession in October 1955 described earlier, suggest that the narrow form is more resistant to conditions unfavorable to the species, and consequently possesses a selective advantage in such circumstances. Further studies on the relationship of the two forms would be interesting.

(b) *Anabaena *spiroides*

This bluegreen alga usually constitutes the greater part of the maximum densities (assessed by cell volume, Fig. 2) that are attained yearly by the phytoplankton. Its main annual increase at measurable densities occurs after the filling of the reservoir basin, but 1–2 months later than the corresponding increase of *Melosira*. The difference may result only from the lower densities of *Anabaena* in the water of the upper river, which bears the "inoculum" for growth in the reservoir basin. Analogous differences between the succession of the species along the reservoir basin (p. 225) may originate in the same way. The *Anabaena* increase is probably not subject to the same limitation which ends that of *Melosira*, as increase in *Anabaena* populations often continues through a period of decrease in *Melosira*.

Rapid increase in the *Anabaena* population is usually halted in November. Later behaviour follows one of two patterns. High or fairly high densities may be maintained, with minor fluctuations, for several months, finally declining in March or later (e.g., 1951–2, 1954–5, 1955–6). Alternately the maximum may be short-lived, and ended by an earlier decline in December to January (e.g., 1952–3, 1953–4). In 1955–6 the persistent maximum was dominated, in the later stages, by filaments in unusually small coils, which suggested a depauperate condition. The existence of such a condition in earlier years is uncertain.

(c) *Lyngbya limnetica*

This alga shows a simple periodicity, with well-defined annual maxima of brief duration. The number of filaments per ml may reach high values, but the corresponding cell volumes are not large owing to the small filament dimensions. The period of increase may coincide with that of *Anabaena *spiroides* (1953), or take place slightly earlier (1951, 1952) or later (1955). Despite these differences, which could result from variations in the proportions of the two species in the upper river "inoculum", the increase of *Lyngbya* usually ceases about the same time as that of *Anabaena*. A common factor, limiting the maximum densities of the two algae, is therefore suggested. Whatever the later behaviour of the *Anabaena*, the decline of the *Lyngbya* population is both early and rapid.

(d) *Other species*

Although many other algae (listed by Brook 1954) occur in the plankton, few attain notable densities or show a regular annual periodicity. *Anabaenopsis tanganyikae* and *A. cunningtonii* occur in some numbers in at least four of the five years studied (Fig. 2). Maxima, of the order of 1000–5000 filaments per ml (about 1.5–7.5 mm^3 cell volume per L), are reached at a relatively late phase in the yearly season of phytoplankton growth.

Other species appeared to be of more irreglar occurrence. The diatom *Synedra acus* Kg. was recorded in small numbers during all years, and in 1951 and 1955 rose to pronounced November maxima of 300 and 700 cells per ml, respectively. This latter maximum occurred at a time when the numbers of the principal diatom, *Melosira*, were de-

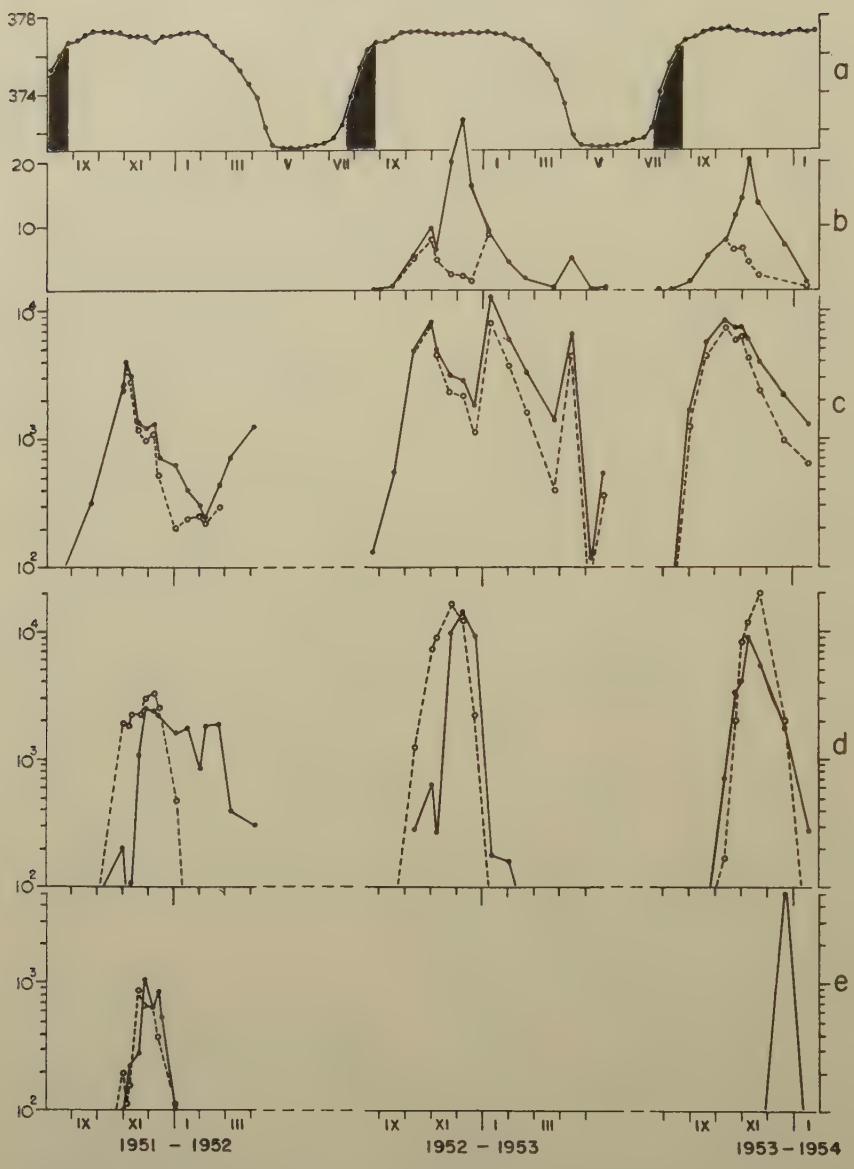

Fig 2A

Fig. 2. Seasonal changes during 1951–6 of water level (m above sea-level) upstream of the dam whose full closure is indicated by black columns (a), and densities of various algae in units of cell volume per L (b) and of individuals per ml (c – e). In (c) – (e) "individuals" of *Melosira* are filaments (1951–2) or cells (1952–6); of *Anabaena* * *spiroides*, filaments (1951–2) or coil-turns (1952–6); of *Lyngbya*, *Anabaenopsis*, and *Anabaena aphanizomenoides*, filaments.

clining. In November of 1951 and 1955 another species of *Anabaena*, *A. aphanizomenoides* Forti, reached notable but short-lived maxima (Fig. 2) of 850 and 1540 filaments per ml (about 1.7 and 3.1 mm^3 cell volume per L), respectively, but had an inconspicuous history in other years. Green algae were relatively unimportant during all years, although species of *Pediastrum* were often present in small numbers.

(e) *Total algal density*

An approximate measure of the total algal density was obtained by summing the cell

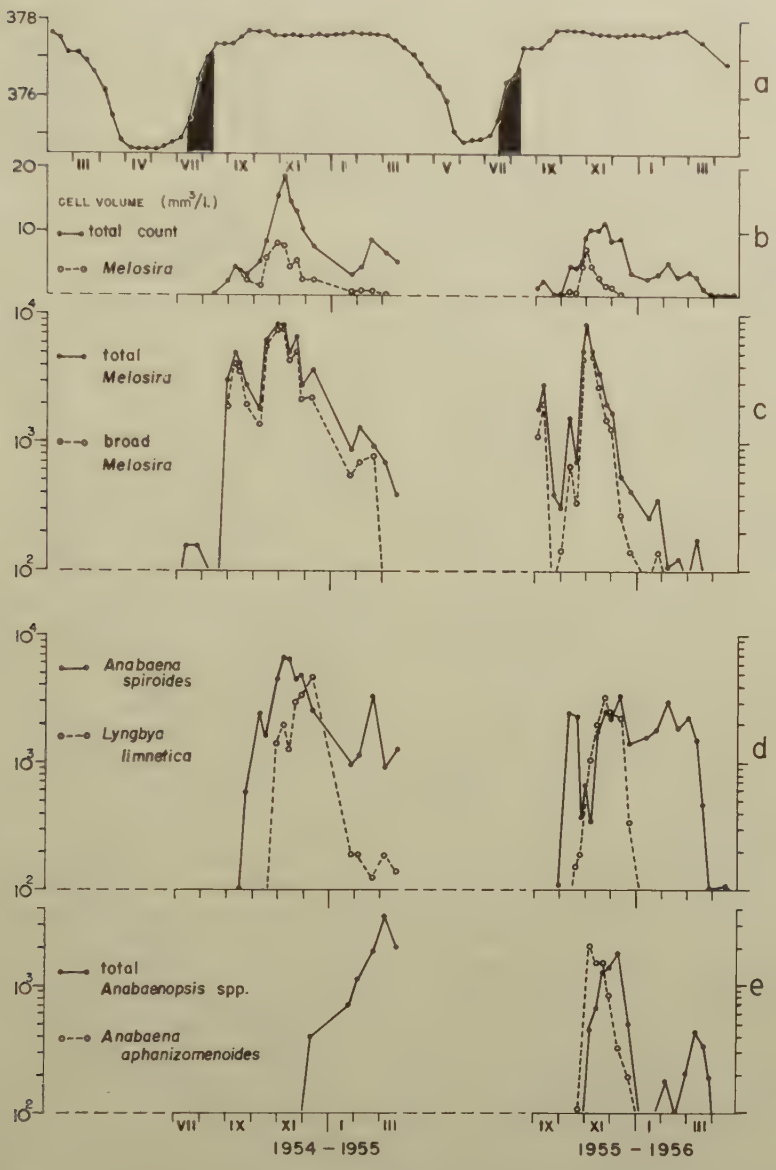

FIG 2B

volumes (determined from cell dimensions), of the principal algae present. The unit of cell volume, 1 mm³, is also very roughly equivalent to 1 mg of dry weight (Table 1; cf. also Ruttner 1937). The seasonal variation (Fig. 2) shows that appreciable densities of algae are realized only during the annual period of water storage in the reservoir basin, as was described by Rzóska *et al.* (1955) from counts of total algal "individuals" (cf. their Figs. 1 and 2). Maximum total densities are usually not reached until November, three months after the primary filling of the reservoir, owing to the time required for growth from the low densities characteristic of the upper river stretches; the exponential nature of the population increase (better shown on the logarithmic scales used for individual species) must also be considered. The expected decline of the total density during the emptying of the reservoir (March–April) is

TABLE 1. *The cell volume and chemical composition of the principal algae*

Species	Unit counted	Volume ($mm^3/10^6$ units)	Dry weight (mg/10^6 units)	Elementary composition (% dry weight)			
				N	P	Si	S
Melosira granulata							
average broad form	cell	1.03	1.12	0.88	0.16	25.3	0.34
average narrow form	cell	0.20	—	—	—	—	—
*Anabaena *spiroides*	coil-turn (ca. 20 cells)	1.60	1.60	7.5	0.28	—	—
Lyngbya limnetica	filament	0.11	—	—	—	—	—
Anabaenopsis tanganyikae	coil-turn	1.30	—	—	—	—	—
Anabaenopsis cunningtonii	filament	1.65	—	—	—	—	—
Synedra acus	cell	0.80	—	—	—	—	—
Anabaena aphanizomenoides	filament	2.00	—	—	—	—	—

* = *A. flos aquae* var. *intermedia* f. *spiroides*

less well documented. It is clear, however, that the main decline usually takes place during an earlier period (December–January) and must be due to other causes.

In all years one diatom, *Melosira granulata*, and one bluegreen alga, *Anabaena *spiroides*, account for most of the volume of algal population. Other bluegreen algae rarely contribute more than 4 mm^3 of cell volume per L and develop mainly in the later part of the growth season. The earlier part is typically dominated by *Melosira*, and the following transition to a dominantly bluegreen community is perhaps the most significant qualitative change in the entire growth season, with implications for the associated animal communities (described briefly by Rzóska *et al.* 1955) and nutrient circulation. The same type of change is evident in longitudinal succession along the reservoir basin, and is emphasized by Brook and Rzóska (1954).

NUTRIENT DEPLETION AND POPULATION MAXIMA

The preceding account of population changes has been largely a descriptive summary of events. Their better understanding requires a more detailed consideration of the physical, chemical, and biological factors involved. The distribution of certain essential nutrients, and the possible significance of their depletion by algal populations, is discussed below. The quantities available are determined by the chemical history of the river water in the upper reaches of the White Nile, which is described by Talling (1957e).

(a) *Inorganic nitrogen*

The availability of inorganic nitrogen is here deduced from the concentration of nitrate nitrogen. Nitrite nitrogen was never detected with certainty, although the sensitive Griess-Ilosvay test was used. Routine estimations of ammonia nitrogen were attempted, but during the periods considered here the concentrations were very small, below 0.04 mg per L, and in a range where the relatively insensitive method used (direct Nesslerization) is neither accurate nor reliable. The larger changes in nitrate nitrogen could be determined down to concentrations of about 0.01 mg per L.

The seasonal variation of nitrate nitrogen during 1954–6 (Fig. 3) shows highest concentrations at the beginning and end of the season of phytoplankton development. A local flush of nitrate from Blue Nile water (p. 224) was demonstrated for 1954. The low concentrations in the intermediate period could arise from uptake by the algal populations or a reduced rate of supply from the upper river region. The latter effect is certainly involved in December, as concentrations in water entering the reservoir were low in December 1953 and 1954 compared to concentrations during June 1954, October 1954, and October 1955. The evidence is derived from Figure 1, Talling (1957e), and unpublished observations. During October there are indications of the depletion of nitrate by algal populations, particularly of *Melosira*. The evidence for this includes (a) a fall in nitrate accompanying the first increase of *Melosira* before the development of *Anabaena*, (b) an inverse correlation between nitrate concentration and *Melosira* density during a *Melosira* maximum in September 1954, (c) a decrease in nitrate parallel with an increase in *Melosira* in a longitudinal section of the reservoir basin (Fig. 1, and p. 226), (d) an approximate equivalence between the combined nitrogen

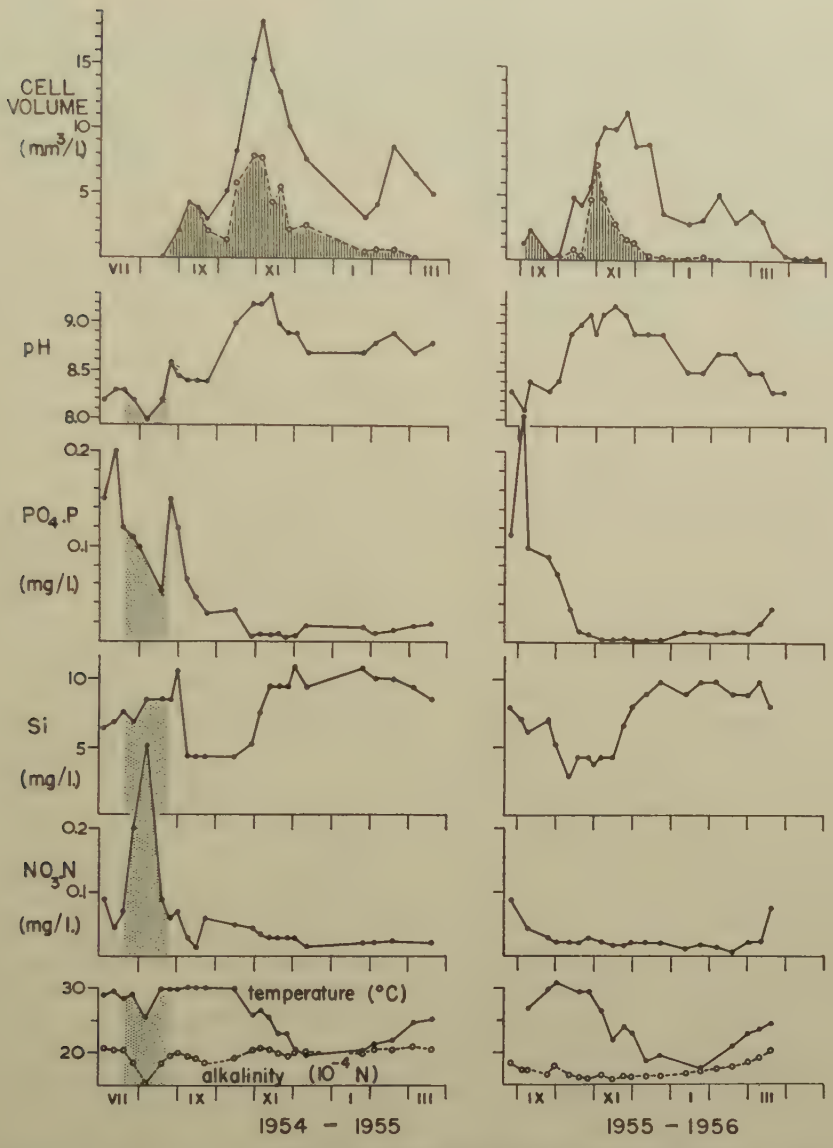

FIG. 3. Seasonal changes during 1954–5 and 1955–6 of algal density (upper graph, with the *Melosira* component shaded) and of various dissolved nutrients (PO_4.P, Si, NO_3.N) and other water characteristics (pH, temperature, alkalinity). Stippled regions indicate periods with admixture of Blue Nile water.

in the maximum *Melosira* crops and the concentrations in the river water entering the reservoir basin; thus in 1954 and 1955 the *Melosira* maxima (October–November) lie between 4 and 8 mm^3 cell volume per L (Fig. 3) or (from Table 1) approximately 4 and 8 mg dry weight per L. These crops may be expected to contain approximately 0.035 to 0.070 mg N per L, using the analysis from the population maximum of 1955 (Table 1). Such quantities of nitrogen are of the same order as the amounts of nitrate nitrogen found in river water entering the head of the reservoir basin (cf. Fig. 1, and Talling 1957d).

If nitrate is the principal source of nitrogen for the *Melosira* populations, and the cell nitrogen content cannot fall much below

the low value (0.88% of the dry weight) recorded, it is likely from Figure 3 that the *Melosira* maxima are limited by nitrogen deficiency. The only cell analysis available, from the population maximum of 1955, shows an unusually low nitrogen content and so suggests possible nitrogen starvation. The periodicity data (Fig. 3) indicate that a concentration of nitrate nitrogen of about 0.02 mg per L may be a critical level for uptake by cells, although it is possible that this level may depend upon population density. The observed minimal concentrations possibly also depend upon rates of regeneration. However, values of about 0.02 mg per L were also associated with an unhealthy and partly declining population of *Melosira* along the reservoir basin during the longitudinal survey of October 1955 (Fig. 1, and p. 226).

The relation between nitrate nitrogen and the nitrogen content of the populations of bluegreen algae (particularly the dominant *Anabaena* **spiroides*) is entirely different. The content in populations of *A.* **spiroides* alone must rise to amounts far higher than the maxima recorded for nitrate nitrogen. The analysis for cell nitrogen (7.5% of the dry weight) is in agreement with other data for bluegreen algae (cf. Lund 1950, Table 1), and implies that the amounts combined in maximum crops during 1954 and 1955 reach 0.7 mg N per L. It seems inevitable that such high requirements must be obtained from other sources of nitrogen, either atmospheric or dissolved organic nitrogen. Data on the fixation of atmospheric nitrogen are not available for the species involved here, but the capacity has been demonstrated in other species of *Anabaena* and *Anabaenopsis* though not of *Lyngbya* (Fogg and Wolf 1955, Table 1). It is noteworthy that the sources of nitrogen utilized by planktonic Myxophyceae in general are far from clear (Lund 1954a, pp. 499–501). Nitrate depletion is unlikely to limit the present *Anabaena* populations, but the latter may well participate in maintaining a low level of nitrate throughout the main growth period.

(b) *Inorganic phosphate*

The seasonal variation of inorganic phosphate also shows evidence of depletion during periods of algal abundance. As with nitrate, changes in the supply from the upper river reaches are also involved, particularly in the decrease from the high concentrations (reaching 0.2 mg $PO_4 \cdot P$ per L) recorded in June to August (Fig. 3, and Talling 1957e). Longitudinal surveys along the reservoir basin, at times when algae were well developed (*i.e.*, December 1953, October and December 1954, and October 1955), generally show a reduction in phosphate from the concentrations in water entering the basin (Fig. 1, Talling 1957e, and unpublished data).

Observations of algal distribution in space and time do not allow this depletion to be analysed with certainty, but there are suggestions of a closer relation to the development of bluegreen algae rather than of *Melosira*. An example is the fall in phosphate and rise in *Anabaena* **spiroides* along the reservoir basin in October 1954 (Fig. 1). If the analysis of the *Anabaena* cells (0.28% P, on a dry weight basis) is representative, the observed population maxima in November 1954 and February 1955 contain approximately half the quantity of inorganic phosphate to be found in an equivalent volume of river water entering the reservoir basin in October 1954 and December 1954, respectively. These concentrations were 0.08 and 0.042 mg per L. There is no proof, however, that the reduction of inorganic phosphate actually limits the population maxima, as in other examples of phytoplankton growth a pronounced depletion is merely accompanied by storage of phosphate in the algal cells in excess of their immediate requirements (Mackereth 1953).

(c) *Silicon*

Changes in dissolved silicon during 1954–6 (Fig. 3) include pronounced minima between September and November. This period is also characterized by the main increase in *Melosira*, the only alga likely to cause a depletion of silicon. Changes of silicon concentration may also result from the variable

discharge of certain upper tributaries rich or poor in this nutrient (Talling 1957e; cf. also Hurst 1957, Fig. 17), but minima would be unlikely to occur at the season under discussion.

In both years the fall in silicon concentration was approximately 5 mg per L. The relation with the increase of *Melosira* does not extend to finer details of timing, or to the quantities of silica estimated (from Table 1) to be incorporated in the diatom populations. These quantities are approximately 1 to 2 mg Si per L for the maxima in 1954 and 1955, respectively. Although less than the total decrease in the open water, the silicon incorporated into dead cells has not been taken into account, nor have possible losses of cells by grazing and sedimentation. These categories may well account for the apparent irregularities, although further examination is clearly desirable. The fall in silica concentration is large in comparison with examples of depletion observed in other waters during diatom maxima (*e.g.*, Lund 1950), although that described by Yoshimura (1939) is of similar magnitude.

(d) *Carbon dioxide and bicarbonate*

Possible sources of the carbon dioxide required in photosynthesis by the algal populations are dissolved carbon dioxide and bicarbonate (cf. Rabinowitch 1951 pp. 888–91, 1956 pp. 1886–92; Ruttner 1953). Uptake of either from the bicarbonate-carbonate buffer system of natural waters results in a rise of pH, the increase being related to the amount of uptake and the alkalinity determined by titration. Such increase in pH is evident during algal growth in 1954–6, from initial values of around 8.2 to maxima of 9.2 or 9.3 (Fig. 3) at times of greatest population density. There is also a pronounced diurnal variation of pH (Talling 1957c), and the maximum values given, from measurements around midday, may slightly underestimate the true maxima to be expected later in the day.

It appears unlikely that high pH, or associated deficiency of carbon dioxide or bicarbonate, ever seriously limits the photosynthesis of the algal populations. Several experiments during the population maximum of 1953 (p. 234) showed that high photosynthetic rates per unit amount of algae could be obtained in river water with initial pH values ranging between 9.2 and 9.5. Higher pH values than these were involved in the limitation of photosynthesis claimed by Steemann Nielsen (1955) for a lake population, and also in other laboratory studies with aquatic plants able to utilize bicarbonate.

(e) *Other nutrients*

The seasonal variation in other nutrients is not known in detail, so that there is no direct evidence for their possible depletion. The concentrations of four nutrients, measured at various times, are as follows: calcium, 8–14 mg per L; magnesium, 8–9 mg per L; sulphate, 1.5 mg per L; potassium (from measurements by Beam 1906, 1908), 4–22 mg per L. Uptake of these nutrients by the algal populations probably involves quantities that are small in comparison with the amounts in solution, with the doubtful exception of sulphate whose true concentration was not measureable. The concentration of total iron is 0.2–0.6 mg per L, but the fraction available for algae is uncertain (cf. Lund 1955b, p. 88). Beauchamp (1953) has suggested that limitation by sulphate deficiency is important for phytoplankton growth in African inland waters, with 0.5 mg per L as an approximate limiting level. More evidence is required (see however Fish 1956) and could be provided by more sensitive measurements of the low sulphate concentrations in the present reservoir. If the sulphur content (Table 1) obtained for one sample of *Anabaena* cells is also characteristic of the population maxima in 1954–6, their sulphate requirements would be of the order of only 0.07 mg per L.

RATES OF PRODUCTION DURING POPULATION MAXIMA

The changes of population density ultimately depend upon rates of increase and depletion of algal substance, assessed per unit of population. The measurement of

rates of depletion (*e.g.*, from grazing and sedimentation) is difficult (Lund and Talling 1957) and was not attempted here, but rates of photosynthetic production were estimated and are described below. Another source of evidence, from the relative growth rates of the populations, could not be used in this work on flowing waters. Rapid rates of relative increase in populations were often recorded, with a doubling of density in 5–10 days during the main phase of population increase. However such increase may reflect only changes in the time available for growth ("retention quotient" of Brook and Woodward 1956) in the reservoir basin, and not the true rate of population growth.

The variation of photosynthetic rate with depth was studied during the algal maximum of 1953–4 (Fig. 4). The results are also used to show variation in maximum rates of photosynthesis per unit of population (P_{max}), and in rates of photosynthetic production per unit area of water surface (Fig. 4) during the decline of the population. These characteristics were also investigated during December 1954 and October 1955 at a station in the reservoir basin, although any variation with algal periodicity could not be followed; the results have been described elsewhere (Talling 1957c).

During the maximum of 1953–4, photosynthetic production at the Gordon's Tree station was largely confined to the uppermost meter stratum. Although light penetration was not measured directly, the variation of photosynthetic rate with depth implies a rapid extinction of light with depth, as was found on later occasions both here and in the reservoir basin (Fig. 1, and Talling 1957c, 1957e). The rates of photosynthesis often exhibit light saturation and occasionally a slight inhibition near the surface. Saturation effects are more prominent in the later experiments, possibly due to the lower temperatures then prevailing (Fig. 4, and Talling 1957a, 1957b).

A separate calculation was made of the maximum (*i.e.*, light saturated) rates of photosynthesis (P_{max}), expressed per unit of cell volume (Table 2). The order of magnitude is similar to that in the later experiments of 1954–5; the range in 1953 is 0.090 ± 0.021, and in 1954–5 is 0.14 ± 0.04 mg oxygen/mm^3·hour. The mean rates are much higher than most values recorded from temperate waters, as pointed out by Talling (1957c). If converted into the units

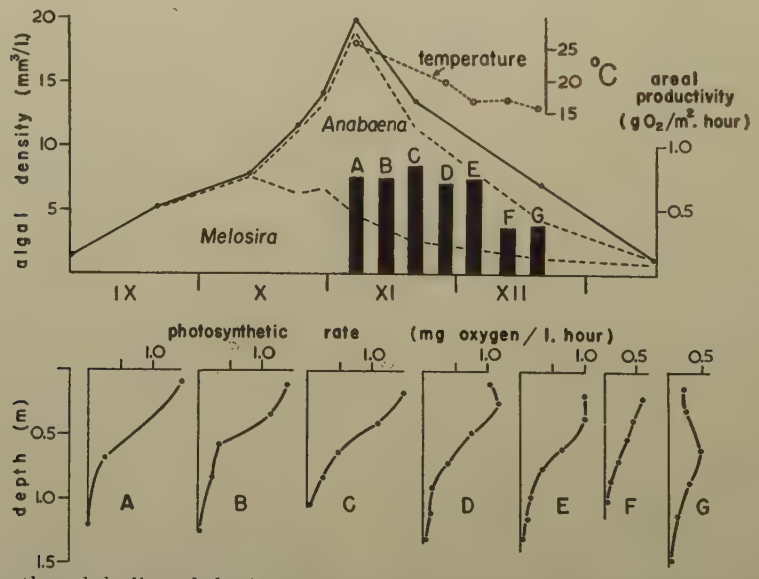

FIG. 4. Growth and decline of the 1953–4 algal population, showing two main components, in mm³ cell volume per L, and of associated rates of photosynthetic production per m² (histograms). The latter are calculated from depth profiles of photosynthetic rate shown in the lower graphs.

TABLE 2. *Photosynthetic rates and productivity under unit area of water surface*

Place and date	Temperature (°C)	Population density (n) (mm^3/L)	Maximum photosynthetic rates		Areal O_2 production near midday (g O_2/m^2. hr)	Estimated daily C fixation (g C/m^3. day)
			n. P_{max} (mg O_2/L. hr)	P_{max} (mg O_2/mm^3. hr)		
A. Gordon's Tree, 40 km below dam						
6. xi. 1953	26	20	1.4	0.072	0.75	2.4
13. xi. 1953	—	17	1.4	0.082	0.75	2.4
20. xi. 1953	—	13.5	1.5	0.11	0.84	2.7
27. xi. 1953	20	12	1.2	0.10	0.71	2.3
4. xii. 1953	17	10.5	1.0	0.10	0.74	2.4
12. xii. 1953	17	6.0	0.59	0.098	0.36	1.15
B. Buoy 1 km south of (*i.e.* above) the Gebel Aulia dam						
19. xii. 1953	16	7.0	0.48	0.069	0.38	1.2
12. xii. 1954	20	5.9	0.60	0.10	0.75	2.4
7. x. 1955	30	1.9	0.35	0.18	0.28	0.90
C. Station 6 km south of (*i.e.* above) the Gebel Aulia dam						
6. x. 1954	30	8.8	1.0	0.12	1.35	4.3

of relative growth rate, assuming an equivalence between the carbon assimilated in photosynthesis and that incorporated in growth, values of the order of 1.6–2.5 cell divisions per day are obtained. This estimation (cf. also Talling 1955, p. 339) assumes a photosynthetic quotient of unity, and a carbon content of 50% of the cell dry weight. Although clearly very approximate, the values obtained are comparable with relative growth rates recorded for a variety of unicellular algae under favourable culture conditions (see, *e.g.*, Myers 1953, p. 44). Because of possible errors involved in algal counts and in estimation of cell volume, the relatively small variation in rates of photosynthesis during the 1953 algal maximum is of doubtful significance. The important feature is that relatively high photosynthetic rates continue into the period of population decline, as was also recorded for the diatom *Asterionella formosa* Hass. at the beginning of population decline in an English lake (Talling 1957a).

Rates of photosynthetic production per unit area (Table 2 and Fig. 4) were calculated by planimetry of the corresponding depth profiles of photosynthetic rate. These areal rates probably approximate the daily maxima, as the experiments were carried out near midday in full sunshine. An analysis of photosynthetic production per day (Talling 1957c, Table 3) suggests that this is approximately 8.5 times the hourly production at midday, under the present conditions of daylength and radiation. To aid comparison with other work, daily production values (in g carbon/m^2·day) have been estimated (Table 2) using this factor and adopting a photosynthetic quotient of unity. The true value of the quotient may well have been higher, probably in the range 1.0–1.4 (cf. Ryther 1956).

Over a period of 30 days during the population maximum the rate of areal production is 0.77 ± 0.07 g oxygen/m^2·/hour as maximum hourly rates, or an estimated 2.4 ± 0.2 g carbon/m^2·day. Later in December there is a decline to approximately half these values, for which decrease in population density and in temperature may be responsible. Changes in the incident daily radiation are relatively small, and its reduction by clouding is negligible. The daily carbon fixation corresponds to the higher rates obtained for phytoplankton in other waters (*e.g.*, Steemann Nielsen 1954, 1956). Similarly high values were obtained from an analysis of diurnal changes of dissolved oxygen in the reservoir basin (Talling 1957c).

Such high productivity is probably only possible in waters where extinction of light by the suspended algae is large (cf. Steemann Nielsen 1954, 1956), so that the unusually shallow photosynthetic zone of about 1 m in the present work is no anomaly.

DISCUSSION

This work is essentially a quantitative description and attempted analysis of phytoplankton development in and below a temporary "river-lake." Plankton development in such water-bodies has received some attention in temperate regions but examples from the tropics and subtropics are rare, although they include a river in Indo-China (Blache 1951) and two reservoir basins elsewhere on the Nile (Abdin 1948, and Rzóska *et al.* 1955). A dominating influence of current velocity is often evident in the yearly periodicity, particularly its reduction during water storage to give lake-like conditions. The causation of later events under such conditions is more obscure, particularly in relation to the succession of species, the limitation of population maxima, and the possible depletion of nutrients.

The limitation of population maxima has been discussed earlier in relation to nutrient depletion, with little attention to physical or biological factors. Temperature changes are probably of little significance here, as a similar pattern of algal periodicity is known for the nearby Blue Nile under different temperature conditions (Rzóska *et al.* 1955, Talling 1956, Prowse and Talling in preparation). The highest temperatures, about 30°C, often occur in the season of most rapid algal increase and so are unlikely to be detrimental. The intensity of the incident radiation does not show marked seasonal changes during the periods considered, and strong absorption of light in the water may not prevent active phytoplankton growth (*e.g.*, in October 1955, Fig. 1). Competition between algae, *e.g.*, for nutrients, is probable, but clearly established examples cannot be cited. Densities of *Melosira* and *Anabaena *spiroides* often show an inverse relationship, but this is not the case during the maximum of 1954–5. The significance of grazing by zooplankton (cf. the review by Edmondson 1957) is unknown. However most of the algal material occurs in relatively large units (*e.g.*, linear filaments of *Melosira*, coiled filaments of *Anabaena *spiroides*), probably too big for direct ingestion by most of the associated Entomostraca and Rotatoria.

The results obtained, and previously described in separate sections, may be summarized as follows. Lake-like conditions, with slow water movement, are created each year on the river after the primary closure of the dam in July to August. Increase in the small phytoplankton population entering the reservoir basin is thereafter evident. The sequence of species in this initial phase of growth, and the timing of the species maxima, are related to their abundance in the inflowing water. *Melosira granulata* is usually predominant here and forms the first species maximum. Its limitation and decline—in which two morphological forms behave differently—is probably due to depletion of inorganic nitrogen, particularly nitrate. Silicon depletion may also occur, but not to limiting levels. A maximum of *Anabaena *spiroides* follows, often accompanied by *Lyngbya limnetica* and sometimes a second maximum of *Melosira*. The total algal densities attained (range 20 ± 8 mm^3 cell volume per L, in November–December) are the highest in the year. They are associated with conspicuous reactions upon some water characteristics, particularly pH, dissolved oxygen, transparency, and inorganic phosphate concentration. Depletion of the latter is most closely connected with the development of *Anabaena *spiroides*, whose large nitrogen requirements appear to be satisfied by sources other than dissolved inorganic nitrogen. Rates of primary (photosynthetic) production at this time are high, estimated as approximately 2.2 g carbon/$m^2 \cdot$day in 1953, despite a shallow photosynthetic zone. The decline of *A. *spiroides* may be early or late, but species of *Anabaenopsis* are usually prominent in the final phase. Other algae are of less regular occurrence, but may show maxima of short duration. The release of storage water in March–April prevents any later growth of

dense phytoplankton, but often the main algal decline occurs much earlier and must be due to other causes.

As storage of water in the reservoir basin is discontinuous, and the water-masses are in movement downstream, conditions are very different from those of a tropical lake with a possibly continuous growth period (cf. p. 222). Nevertheless the results suggest that large oscillations of population density may well occur in tropical lakes as a result of nutrient depletion, with catastrophic decline in the populations. An alternative behaviour, with high densities persisting for long periods after their original limitation, is also illustrated by *Anabaena *spiroides*.

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A Pushnet for Quantitative Sampling of Shrimp in Shallow Estuaries

The shallow estuaries and bayous of the Gulf Coast are used extensively as nursery grounds by several species of commercially important shrimp. In our studies on the estuarine phase of the life cycles of *Penaeus setiferus* and *Penaeus aztecus*, sampling for post-larval and juvenile shrimp in the nursery areas presents a problem. The young shrimp tend to concentrate in areas of stiff salt-cord grass (*Spartina alterniflora*) where it is difficult to operate a beach seine efficiently.

Strawn (1954) describes a one-man pushnet used in shallow water grass flats by Florida bait shrimp fishermen and demonstrates its superiority over a seine for collecting in rooted vegetation. However, the Florida-type net apparently operates most efficiently in submergent vegetation such as turtle grass (*Thalassia testudinum*), which is less rigid than the salt-cord grass. Moreover, it was considered possible that repeated sampling with this net could excessively alter or disturb the stations of limited size occurring in our study area. Finally, we felt that a satisfactory index of abundance, based on a standardized unit of effort, could not be obtained using the Florida net.

Since it appeared that no existing gear was satisfactory for our sampling program, a new type pushnet was developed. This net was designed to yield quantitative samples while being operated by one man in stiff, rooted vegetation in depths of from 3 to 18 inches.

The pushnet described here consists of three units: the handle, the yoke and runners, and the net frame. Figure 1 shows the complete assembly with the major dimensions. The handle is made of 1½ inch aluminum tubing with a wooden crosspiece at the upper end. The yoke (Fig. 1) is a U-shaped pipe, with a short extension welded to the center to receive the handle. The angle of the yoke to the runner is fixed at 30° by a pipe welded in place between the back of the runner and the yoke (Fig. 2). The tubing used for construction of the yoke in this model consists of electrical conduit, though other material such as ¾ inch aluminum tubing would be stronger and lighter. At a point immediately in front of each arm of the yoke, a 4 x 4 inch T-plate, for attaching the net frame, is welded to the runner (Fig. 2). The runners are made of 12 or 16 gauge angle iron 1½ inches wide. The toes of the runners are four inches long and are bent upwards at approximately a 50° angle. A ½ inch galvanized pipe is welded across the bases of the runner toes, approximately one inch above the bottom, to act as a bumper for the net frame. The net frame is made of ¾ x ¾ inch white pine, and the net is attached by thin strips of wood tacked to the inside of the frame. The total weight of the pushnet is approximately 12 pounds and is thus easily operated by one person.

In assembling the pushnet, the male connection of the yoke is inserted into the handle and secured in place by two bolts (Fig. 1). The net frame is attached to the runners by two pairs of bolts through the free portion of the T-plates welded to the runners. All bolts are fitted with wing-nuts to facilitate dismantling or changing nets.

In actual use, the pushnet is pushed at a standard pace for a prescribed measured distance at each station. The weight and relatively narrow width of the pushnet tend to keep it on the bottom. The bumper bar, while protecting the net frame, also serves to dislodge many organisms from the vegetation. The net frame, fixed to and stabilized by the runners, fishes at a constant angle. The method of collecting is thus standardized, and it is our opinion that samples obtained in this manner are quantitative.

Samples collected over a period of five months, using No. 20 woven nylon mesh, contained considerable numbers of invertebrates and fishes. However, from our observations, repeated sampling at weekly intervals did not appreciably alter the stations.

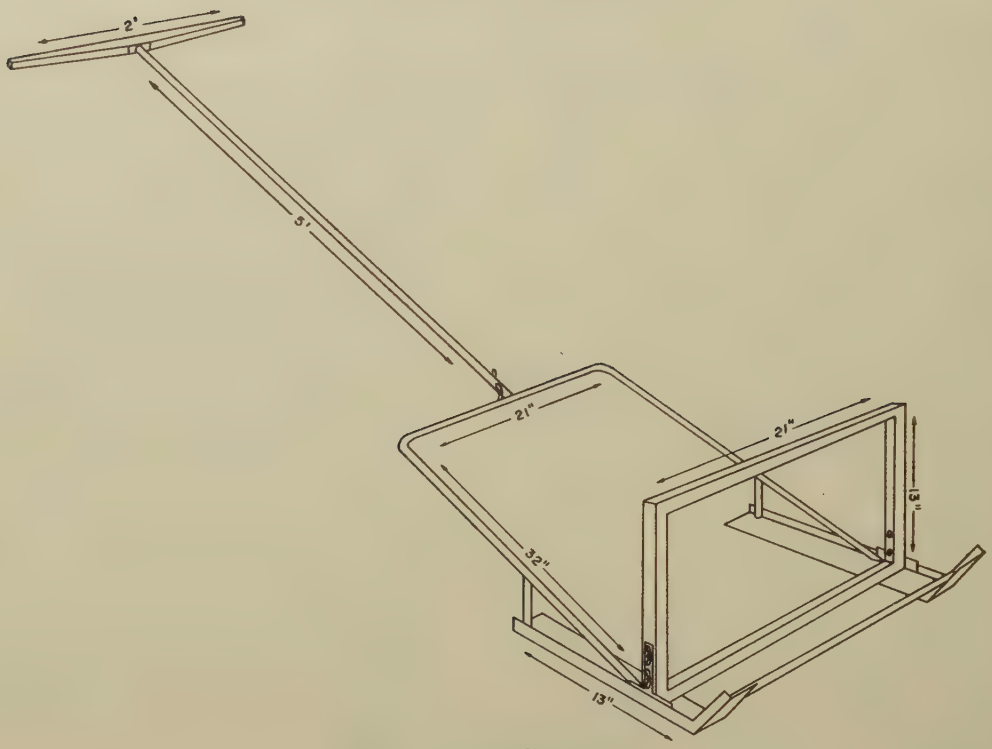

FIG. 1. Pushnet dimensions.

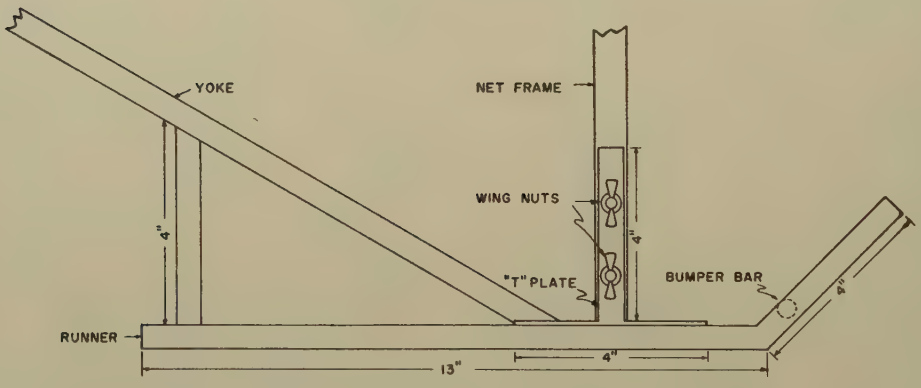

FIG. 2. Side view of pushnet showing construction detail.

We caught penaeid shrimp ranging in length from 6 to 85 mm in beds of partially inundated salt-cord grass as well as in shallow water devoid of vegetation. Shrimp larger than 85 mm probably did not commonly occur in these shallow water stations, since they were never seen leaping to avoid the net, as were the smaller shrimp.

It is considered possible, however, that the pushnet cannot capture the larger shrimp of the 6 to 85 mm size range in proportion to their actual abundance. Furthermore, *Penaeus setiferus* may be more adept than *Penaeus aztecus* in avoiding this net. De Sylva (1954) mentions this same possibility with reference to the Florida pushnet.

Attempts were made to determine the selectivity of the pushnet with reference to the size and species of shrimp. Both the pushnet and a 20-foot seine were operated within a shallow grassy area. The results, however, were inconclusive, since

the inefficient functioning of the seine made comparison of the catch between the two types of gear impossible.

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BOOK REVIEWS

GESSNER, FRITZ, AND VOLKMAR VARESCHI (Editors). 1956. **Ergebnisse der deutschen limnologischen Venezuela-Expedition 1952. Bd. I.** VEB Deutscher Verlag der Wissenschaften, Berlin. viii + 360 pp. DM 40 (approx. $9.60).

Gessner went to Caracas in September 1952 to attend the meeting of the International Union for the Protection of Nature, and stayed on for three months afterward to study the limnology of Venezuela. With Vareschi as contact man and co-worker, in addition to brief local trips in the vicinity of Caracas they visited Lake Valencia, Lake Maracaibo, the lower Orinoco River, the Andes west of Maracaibo, and the Los Aves islands north of the mainland. Moreover, on his return to Germany by freighter Gessner was able to collect additional material along the lower portion of the Magdalena River in Colombia. The expedition was run on a slim margin financially. Many times Gessner and Vareschi were dependent upon the hospitality of local persons and firms, and much of the cost was financed by lectures Gessner presented at Caracas and Merida.

With this background it is understandable that much of the effort was devoted to collecting the biota from the wide range of habitats visited. Only spot limnological observations could be made, not nearly so extensive as those of the German Limnological Sunda Expedition, and hence our knowledge of the seasonal limnology of the tropics is still very deficient.

The specimens collected were sent to various recognized specialists, and their reports form the bulk of the first volume. Relatively little had been known previously about the aquatic biota of Venezuela, and the present volume contributes much to this aspect of limnology. Many new species are described. In honor of the organizer of the expedition the specific name *Gessneri* has been used over and over again in all the various groups of algae and animals.

Gessner himself describes the plankton of Lake Maracaibo, which is dominated by *Microcystis*. Characteristic of the plankton is the very unequal horizontal distribution, governed in part by the salinity gradient. The lake is oligohaline, and this together with the high temperatures (>30°C) results in stratification with the bottom water tending to be deficient in oxygen. The plankton as a consequence also exhibits a non-homogeneous vertical distribution.

Vareschi has a paper on the phytogeography of Venezuela. Five vegetational units are described and mapped: 1) tropical rain forest formation, 2) mangrove forest formation, 3) mountain forest vegetational region, 4) Passat forests vegetational region, and 5) cactus steppe vegetational region. The Passat forests, which cover about ¾ of the total area of the country, have an aspect similar to the monsoon forests of India, although the dry seasons in Venezuela are not controlled by monsoon winds. Of special limnological interest are the falls of the Rio Caroni where it joins the Orinoco. This region is rich in Podostemonaceae.

Pannier presents climatograms for a number of localities of contrasting climate. In a climatogram the mean monthly precipitation and mean temperature are plotted for the year, with 20 mm of precipitation having the same scale value as 10°C of temperature. The relationship of the two curves with respect to each other is used in helping describe the local climate.

Hustedt lists 125 species and 4 forms of diatoms, of which 27 are new. The genus *Nitzchia* is clearly dominant in this region, although in Lake Maracaibo the dominants are *Melosira ambigua* and *Nitzschia palea*, the latter living in the gelatinous envelopes of the *Microcystis* colonies. The salinity, even though small, is the chief controlling environmental factor.

Krieger and Bourrelly found 190 species and lesser categories of desmids, in which *Cosmarium* is dominant, followed by *Euastrum* and *Staurastrum*. They described 23 new varieties and species, mostly the former.

On the Los Aves coral islands some distance off the coast large nesting colonies of gannets have formed extensive guano deposits. Along the margins of the islands are small spray pools, heavily fertilized by the gannet excrement, and in which there are large fluctuations in temperature and salinity. Most of these pools are blood red in color from a dinoflagellate, described here as *Haematodinium Gessneri* in a new genus and a new family. In addition 12 other new species and 3 new genera of algae are described from this interesting microhabitat.

Brehm lists 1 species of Conchostraca and 31 species and varieties of Cladocera. *Bosmina tubicen* is described as a fifth valid species in this highly variable genus. *Daphnia* was found only at high altitudes, which strengthens the previous belief that this genus does not commonly occur at low altitudes in the tropics. Brehm placed two vastly different specimens of *Alonella* in the same species, which seems to the reviewer as probably in error. In his experience the various species of *Alonella* are very stable in their adult morphology.

Very little was known previously about the cyclopoids and calanoids in northern South America. Kiefer in this volume records 20 species and subspecies—4 calanoids and 16 cyclopoids—of which 2 calanoids and 5 cyclopoids are new. In contrast to some of the other groups of freshwater organisms, there is a high degree of endemism in these two groups. Fourteen species and subspecies are known only from South and Middle America.

Chappuis identified the 2 species of harpacti-

coids in the collections, both of them in the genus *Attheyella*, one of them being new. Both were collected in the leaf axils of *Heliconia* in the rain forest at an altitude of about 1000 m.

Hauer lists about 100 species of rotifers, including 5 new species and 1 new variety. There are few geographic barriers to distribution in this phylum, most of the local control being exercised by ecological factors.

Karl Viets studied the Hydrachnellae in the collections. Thirty-four specimens were distributed among 14 species, of which 5 are new. Three of these are described on the basis of just 1 specimen each, and the other 2 on just 2 specimens each! Both Gessner and Viets comment about the extreme sparseness of water mites in the Venezuelan material.

Van Oye described 2 new genera, 9 new species, and 3 new varieties of testaceous rhizopods (thekamoebae). The list of species increases the number of species known from Venezuela from 76 to 109. *Difflugia* is rather poorly represented. The fauna as a whole differs quite widely from those of Europe and North America, and resembles more closely those of Africa and Australia.

Most specialists discussed the biogeographic aspects of their groups. Brehm, especially, relied rather strongly on land bridges, even though these are now generally discredited in biogeographic speculation.

Thus, the results as presented in this first volume consist mainly of taxonomic treatises of the organisms collected, with relatively little that contributes to our knowledge of limnological processes in the tropics.

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